

The University of Chicago

STUDIES ON TRANSPLANTATION  
IN *PLANARIA*

A DISSERTATION SUBMITTED TO THE  
GRADUATE FACULTY IN CANDIDACY FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOÖLOGY

By  
FELIX V. SANTOS

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## STUDIES ON TRANSPLANTATION IN PLANARIA

(Seventy figures)

FELIX V. SANTOS  
University of Chicago

### INTRODUCTION

**D**URING the last three years the writer has been engaged in a study of transplantation in *Planaria*. The object of this research was, first, to determine the effect or influence of the graft on the host and of the host on the graft; and second, to determine how the different levels or regions of the body of *Planaria* differ (*a*) as host and (*b*) as graft. The investigation was suggested by Dr. C. M. Child, and the work has been carried on under his direction. The writer wishes to acknowledge his indebtedness to Dr. C. M. Child for suggestions and criticisms.

Some of the questions that arose in the course of this investigation and furnished additional stimulus in the carrying-out of this research are: (1) Does the fate of the graft depend upon the degree of specialization, or does it depend upon the degree of physiological activity of the graft? (2) Does the active dominant region of the planarian body, such as the head or ganglionic region of the head (Child, 1929*b*), act as an organizer when transplanted into a relatively less active region of the body? (3) Is its effect species-specific? (4) On what factors does the fate of the graft depend? The work was undertaken in the hope of throwing additional light on the dynamics of histogenesis and of morphogenesis. Some of the more important results obtained thus far have already been briefly discussed in the preliminary paper (Santos, 1929).

Most of the earlier work on transplantation in the lower invertebrates has been chiefly concerned with other problems than those which are attacked in the present paper. Various investigators have grafted together pieces of hydroids, *Turbellaria*, or annelids in various positions. When such grafts are made in reversed polar orientation with respect to each other and one component is made much

smaller than the other, either at the time of grafting or by subsequent removal of a part, the polarity of the smaller component is often reversed. Such experiments, however, do not necessarily demonstrate induction by the larger component, for short isolated pieces of the species concerned often give rise to bipolar forms; and the reversal of polarity in the shorter components of the grafts in reversed position may represent merely the effect of the posterior or anterior cut surfaces in determining a new polarity, and inhibition of development at the anterior or posterior cut surface by union with the other component. Various other cases of alteration of polarity, or symmetry in consequence of transplantation, or of other operations which alter the positions and relations of parts to each other have been reported. The recent work of Spemann and his collaborators on the so-called "organizer" of the urodele embryo has greatly stimulated interest in the problem of the physiological relations of parts to each other in embryonic development and reconstitution; and "induction," that is, organizing or reorganizing action of a part or region on others, has been discovered or postulated in numerous cases. It is impossible to consider all such cases here; furthermore, recent general papers make such consideration unnecessary. For example, in the *Festschrift* for Spemann, Korschelt (1929) discusses morphogenetic induction, Goetsch (1929) the experimental influencing of regeneration, and Child (1929*b*) physiological dominance; and all of these papers give extensive bibliographies. It may perhaps be questioned whether certain cases which have been regarded as cases of induction, and particularly certain cases of reversal of polarity of anterior or distal regions by posterior or proximal regions, are really such; but the fact that certain regions are physiologically dominant over others and that such regions do exert an organizing or reorganizing action or induction in embryonic development and in reconstitution cannot be doubted. This action or influence appears both in the determination of the development of certain parts and in the prevention of development of others, but it is not necessary to assume that these two effects result from different physiological factors. The prevention or inhibition by a dominant region, or organizer of a certain sort of development in a certain region, undoubtedly results not from an actual inhibiting action



on the part of the dominant region but from the determination in the region concerned of some other line of development.

A few of the more striking cases of the morphogenetic effects of physiological dominance among the lower invertebrates are briefly mentioned. Browne (1909) found that even small pieces from the hypostome region of *Hydra*, transplanted to other regions of the host body, might determine a new apical region and axis. By using individuals of different colors as host and donor, she was able to show that the new individual determined by the graft developed in large part from the host body. Small pieces from other regions of the body had no such determining or inducing effect, but large pieces might persist and give rise to apical ends and new axes. Rand, Bovard, and Minnich (1926) have obtained similar results. The experiments of Goetsch (1922-26, 1929) on *Hydra* and other hydroids give further data concerning actual or postulated organizing action in these forms.

In the case of *Corymorpha*, Child (1929a) showed that even a very small piece of the stem grafted into a lateral incision in the stem of another individual would induce development of a new hydranth and stem, the graft forming only the apical portion of the hydranth.

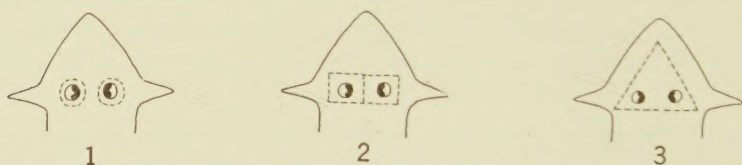
Most cases of induction in planarians which have been reported by earlier investigators consist in the prevention of development of a head or a posterior end when the relations of the region concerned to other parts, and particularly to a head region, are altered either by transplantation or by certain other operations. Various cases of this sort are mentioned by Korschelt (1929), Goetsch (1929), Rand and Ellis (1926), and Rand and Browne (1926); and Yiking Li (1928) also describes cases of this sort.

Previous investigators, however, have presented little evidence for actual organizing action or induction, that is, the determination of development of new parts by a transplanted part, e.g., a head. Some of the cases of heads developed from transplanted regenerating tissue described by Gebhardt (1926) suggest that the graft has organized or determined some slight outgrowth from the host body, but Gebhardt does not discuss this point. In some of the experiments of Goetsch (1929, pp. 264-66) the evidence is more conclusive.

In these experiments regenerating head regions were transplanted, and later the region of the host body about the transplant was isolated by section. The grafted head was often able to prevent entirely or in part the development of a head on the piece of the host body and also to reorganize the piece into an elongated structure, apparently a postcephalic region.

#### MATERIALS AND METHODS

*Planaria dorocephala* Woodworth and the form commonly known as *P. maculata* Leidy were the animals used in this work. The latter species was obtained from the vicinity of New Haven and from Woods Hole through the kindness of Dr. L. G. Barth and Dr. J. W. Buchanan. The sizes of the worms used range from 10 to



FIGS. 1-3.—Planarian heads showing regions, shapes, and sizes of pieces used as ganglionic grafts.

22 mm. in length. A saturated aqueous solution of chloretone diluted with four parts of well water or a weak aqueous solution of chloretone (ca. M/100) was used in most cases as anesthetic. The donors were not anesthetized. In some cases neither the host nor the donor was anesthetized. In many of the earlier experiments circular grafts (Fig. 1) about  $\frac{1}{2}$  mm. in diameter were cut by means of a capillary pipette and inserted into a hole in the host body with the same pipette. In other cases rectangular pieces representing either approximately a half or the whole of the ganglionic region (Fig. 2) were cut with a sharp scalpel and inserted into rectangular holes of as nearly as possible the same size. In the course of the experiments, however, it was found that triangular pieces were the most satisfactory. With pieces cut in the form of isosceles triangles, with the sides longer than the base, and implanted into a hole of approximately the same size and shape, definite orientation with respect to the polar axis of the donor and host is possible. In the case of the ganglionic region, equilateral triangular pieces were used, the presence of the eyes mak-



ing orientation possible (Fig. 3). Since the polarity of the graft and its effect on the polarity of the host are important features of the investigation, the advantages of the triangular pieces as grafts are obvious. The operated worms were kept in the dark, in moist chambers consisting of finger bowls and small watch glasses with very little well water, only enough to keep the worms moist, for about 12-24 hours immediately following the operation. After this length of time, those with successful grafts were examined under a binocular microscope, counted, recorded, and transferred into finger bowls with *ca.* 200 cc. fresh well water, covered with glass plates, and kept in the dark in the usual way. In some of the experiments the host was beheaded, to keep it relatively quiet and thus increase the percentage of "takes"; while in other cases the host was not beheaded. Both homoplastic transplantation and heteroplastic transplantation were performed, the latter between *Planaria dorotocephala* and *P. maculata*. In some of the experiments *P. maculata* was the host, while in others the host was *P. dorotocephala*. The region of the cephalic ganglia and various levels of the prepharyngeal, pharyngeal, and postpharyngeal regions were the different levels of the body that have been used as graft and, with the exception of the ganglionic region, as region of implantation in these experiments. The grafted piece was either transplanted without its axis being rotated or the axis of the transplanted piece was rotated  $60^{\circ}$ - $180^{\circ}$ . In some cases the piece was grafted with its dorsal surface toward the ventral surface of the host.

In general, the experimental animals which were able to feed were fed with beef liver two or three times a week. The pattern of the gut in the experimental animals has been determined either by examining the living animals under slight pressure with strong light and small diaphragm or by feeding the animals clotted blood. The parts of the gut which are filled from a particular pharynx in feeding and the movements of the gut contents serve to show the connections between the various parts of the reorganized guts.

The figures are semidiagrammatic outlines drawn in each case from the living animal to show the essential features of the results obtained. No attempt is made to indicate the actual difference in size of the animals in the figures. Some of the figures are drawn on a

somewhat larger scale than others in order to show clearly the essential points. Since no characteristic difference in results in relation to size of animals has been observed, this variation in scale of figures is regarded as justifiable. In the figures, the pharynx serves as a landmark and as evidence of induced reorganization. The reorganization of the gut in relation to the new pharynxes is not shown in the figures but will be considered in a later paper in connection with the histological data.

#### GRAFTS OF THE GANGLIONIC REGION

*Homoplastic grafts of the ganglionic region of Planaria dorotocephala.*—The more important results obtained with homoplastic grafts of the ganglionic region of *Planaria dorotocephala* are summarized in Table I. The table does not include all the experiments performed with ganglionic grafts. In many of the earlier experiments with small circular or rectangular grafts (Figs. 1 and 2) complete resorption of the graft took place. Since the development of a head and the induction of an outgrowth by the graft were considered to be of greater interest than resorption, most of these experiments are not recorded in Table I. Some other experiments with the large triangular pieces (Fig. 3) in which only small numbers of animals were used are also omitted from Table I.

The table is in large part a record of the data obtained after the technique had been satisfactorily developed, and represents the entire range of results observed. For purposes of tabulation various series of experiments performed at different times in which implantation was made at approximately the same level of the body are combined under a single series number. The consecutive series numbers in the table represent successive levels of the body from the anterior prepharyngeal region posteriorly, as indicated in the third column. The fourth and fifth columns of the table give the numbers of successful grafts ("takes") and the numbers of unsuccessful cases ("non-takes") which were used as controls. The sixth column gives the cases in which at least some degree of development of a head from the graft and induction of an outgrowth occurred. Cases of resorption are not tabulated, since only two cases occurred (Series 5) among the experiments recorded in the table.

In many experiments the anterior end of the host was removed at a level somewhat anterior to the level of implantation after development of the graft head and induction of an outgrowth by the graft had taken place. Usually such removal is followed by development

TABLE I  
HOMOPLASTIC GRAFTS OF GANGLIONIC REGION,  
*Planaria dorotocephala*, LENGTH 10-22 MM.

| Series | Shape and Size of Graft                    | Level of Implantation               | Number of "Takes" | Controls ("Non-Takes") | Induction of Outgrowth         | Subsequent Removal of Anterior Part of Host | Head of Host Inhibited | Reversal of Polarity in Host |
|--------|--------------------------------------------|-------------------------------------|-------------------|------------------------|--------------------------------|---------------------------------------------|------------------------|------------------------------|
| 1....  | Circular, one-half ganglion                | Anterior prepharyngeal              | 7                 | 23                     | 7                              | 7                                           | 5                      | .....                        |
| 2....  | Rectangular, or triangular, whole ganglion | Middle prepharyngeal                | 53                | 21                     | 53                             | 16                                          | 0                      | .....                        |
| 3....  | Rectangular, whole ganglion                | Posterior prepharyngeal             | 38                | 11                     | 38                             | 17                                          | 5                      | .....                        |
| 4....  | Triangular, whole ganglion                 | Pharyngeal                          | 31                | 17                     | 31<br>(22 with 2 pharynxes)    | .....                                       | .....                  | .....                        |
| 5....  | Rectangular or triangular                  | Middle postpharyngeal               | 52                | 84                     | 50<br>(13 with second pharynx) | .....                                       | .....                  | .....                        |
| 6....  | Triangular, whole ganglion                 | Middle and posterior postpharyngeal | 125               | 75                     | 125                            | 125                                         | 59                     | 113                          |

of a new head, which may be more or less inhibited in its development. Removal of this reconstituted head may be followed by development of another head still more inhibited or by complete inhibition of head development at the anterior cut end of the host. After a third removal, head development is usually completely prevented. When the level of removal of the anterior end of the host is near the level of the graft, the effect of the graft in inhibiting



development of a new head is greater and fewer removals are necessary for complete inhibition of head development. Also, the more completely developed graft heads are in general more effective in inhibiting head development at more anterior levels than those which are less developed. And finally, ganglionic grafts in the postpharyngeal region are apparently more effective in inhibiting head development at levels of the host body anterior to the graft level than are such grafts in the prepharyngeal region.

In Table I the number of cases in which the anterior end of the host was removed once or more than once (number of removals not given in table) is given in the seventh column; and the number of cases in which development of a new head was inhibited or prevented, in the eighth column. The data show that such inhibition or prevention of head development is much more frequent in the case of grafts in the postpharyngeal than with prepharyngeal grafts. More extended consideration of this effect of the graft head in inhibiting head development at levels of the host body anterior to it is reserved for a later paper, in which data will be presented to show the gradual increase in this effect in particular cases.

When ganglionic grafts are implanted into the posterior part of the postpharyngeal region, a reversal of polarity in at least part of the host body is often induced by the graft. The cases of such reversal are recorded in the last column of Table I.

In general, it may be stated that the results of grafting pieces from the ganglionic region are always resorption when the pieces are below a certain size, or some degree of development from the graft of a head region which may be highly abnormal in form; and, except when implantation is very near the head of the host, induction of an outgrowth from the tissue of the host which represents more or less of the postcephalic region. In no case observed, however, does this induced body include regions posterior to the level of implantation.

Detailed consideration of all cases is, of course, impossible; but description of a number of cases selected from the data will serve to illustrate the character and range of variation of the results obtained with these homoplastic grafts of the ganglionic region. Figures 4 and 5 represent a case of implantation in the anterior prepharyngeal region just posterior to the head of the host (Series 1, Table I), the

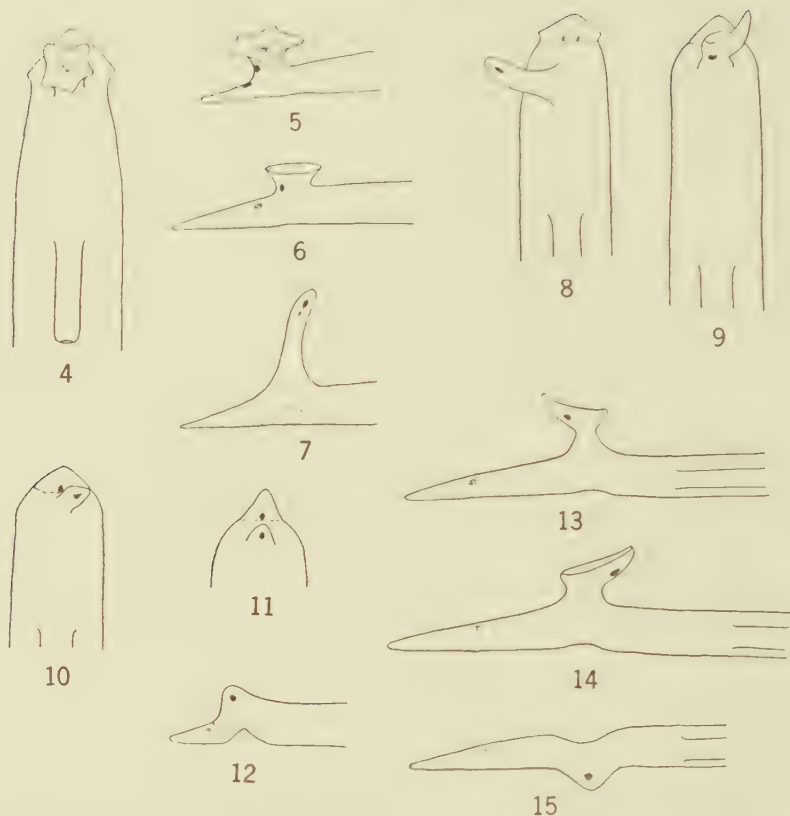
graft being implanted in reversed dorsoventral orientation. A highly abnormal head region developed with ventral surface consisting of the characteristic ventral epithelium uppermost. In Figure 5 the position of the eyes of the host and the single eye of the graft are indicated. The ventral surface of the reconstituted head region is concave, and the margin shows five pointed outgrowths. It was impossible to determine with certainty whether a particular one or each of these outgrowths represented an anterior tip. All five underwent contraction and extension simultaneously, and it seems possible that they all represent anterior tips and that this head region is multipolar to that extent.

Figure 6 shows a case somewhat similar to the preceding. The graft was implanted just posterior to the head in reversed dorsoventral orientation. The head region which develops from the graft is funnel-shaped with ventral epithelium on the inner, and dorsal epithelium on the outer, surface of the funnel.

In Figures 7 and 8 a case of implantation into the anterior prepharyngeal region (Series 1, Table I) with normal dorsoventral orientation is shown. Figure 7 is a lateral view; and Figure 8, a dorsal view with the outgrowth bent to one side. The outgrowth is cylindrical and covered with epithelium like that of the dorsal surface, but the eyespot indicates that its free end represents a head region. The ventral surface of the host at the level of the graft is concave in the dorsal direction. In this case the head of the host was removed after development of the outgrowth; but the development of a new head took place, as indicated in Figure 8.

Figure 9, another case of implantation with normal dorsoventral orientation in the anterior prepharyngeal region (Series 1, Table I), shows development of a highly abnormal head with a tapering outgrowth on one side. Here, also, the head of the host was removed after development of the graft, and a new head developed as indicated in the figure.

In Figure 10 another case from the anterior prepharyngeal region (Series 1, Table I) with normal dorsoventral orientation is shown, but the level of implantation is slightly more posterior than in the preceding cases. Here the head which develops from the graft is more nearly normal in form, and a short outgrowth posterior to it



FIGS. 4-15.—*Planaria dorotocephala*. Homoplastic ganglionic grafts in anterior and middle prepharyngeal regions.

Figs. 4-6, circular grafts in anterior prepharyngeal region, normal anteroposterior, reversed dorsoventral orientation. Union incomplete. Figs. 4 and 5, dorsal and lateral views of the same graft. Fig. 6, another similar graft.

Figs. 7 and 8, circular graft in anterior prepharyngeal region in normal orientation, union complete. Graft head covered with dorsal epithelium. Graft has induced post-cephalic outgrowth. Fig. 7, lateral view; Fig. 8, dorsal view with graft bent to one side. Head of host removed after development of graft and development of new head not inhibited.

Fig. 9, triangular graft in anterior prepharyngeal region, in reversed anteroposterior and dorsoventral orientation, union incomplete. Head of host removed after development of graft, and new head partially inhibited.

Figs. 10-12, circular grafts in anterior prepharyngeal region in normal orientation. Union complete, graft head covered with dorsal epithelium. Head of host removed after development of graft, and new head partially inhibited. Fig. 11, dorsal view; Fig. 12, lateral view of same graft.

Figs. 13-15, triangular grafts in middle prepharyngeal region. Fig. 13, in normal anteroposterior, reversed dorsoventral orientation. Union incomplete. Fig. 14, in reversed anteroposterior and dorsoventral orientation. Union incomplete. Fig. 15, in normal orientation, union complete, graft head ventral, covered with ventral epithelium.



has arisen. The head of the host was removed after the graft developed; and the new head is somewhat inhibited, as is indicated by the median eyespot. Figures 11 and 12 are dorsal and lateral views of a similar case but with less outgrowth. Here, also, the head of the host was removed after development of the graft; and the new head is partially inhibited in development, as its form and the single median eye indicate (Fig. 11).

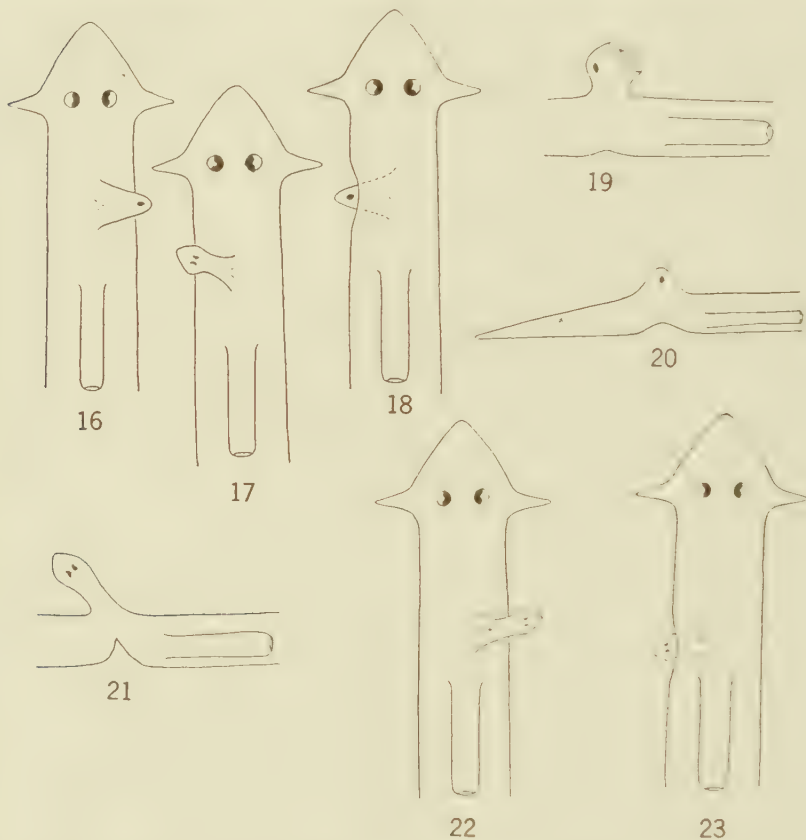
Figures 13 and 14 show two cases of implantation into the middle prepharyngeal region (Series 2, Table I) with reversed dorsoventral orientation and, in the case of Figure 14, with reversed antero-posterior orientation. In both cases the head develops from the graft with ventral epithelium on the concave upper surface; and in Figure 14, with its anterior end directed toward the posterior end of the host. In these cases the head of the host was not removed. In the case shown in Figure 15 the graft was implanted in normal position; but the head developed on the ventral side of the host, and the dorsal surface of the host became concave in the region of the graft. Here, also, the head of the host was not removed.

Figures 16, 17, and 18 show further cases of implantation in the middle prepharyngeal region (Series 2, Table I) with normal orientation of the graft. In Figures 16 and 17 the head and outgrowth develop on the dorsal surface of the host, and in Figure 18, on the ventral surface. In these cases the head of the host was not removed.

In Figures 19, 20, 21, 22, and 23 cases of implantation into the posterior part of the prepharyngeal region (Series 3, Table I) are shown. In the case of Figure 19 the graft was in reversed dorsoventral orientation; and, as in other cases with similar orientation described above, the head develops with ventral epithelium on the concave upper surface. Figures 20-22 show cases with normal orientation of graft and development of head and outgrowth on the dorsal surface of the host. In the case of Figure 23 the graft was implanted in reversed dorsoventral orientation, and the head and outgrowth developed on the ventral surface of the host. The head of the host was not removed in any of these cases.

Grafts of the ganglionic region into the pharyngeal region (Series 4, Table I) also developed a prepharyngeal region from the host body. In most cases, also, development of a second pharynx in the host body was induced. One of these cases is shown in Figure 24.

Here the pharyngeal region of the host was completely removed and replaced by the graft. The host has developed a new pharynx, and the graft has induced development of a cylindrical prepharyngeal



FIGS. 16-23.—*Planaria dorotocephala*. Triangular, homoplastic grafts in middle and posterior prepharyngeal region.

Figs. 16-18, grafts in middle prepharyngeal region. Dorsal views with outgrowth bent to one side, normal orientation. Fig. 16, union complete, graft head covered with dorsal epithelium. Fig. 17, union incomplete, head normal. Fig. 18, union complete, graft head ventral, covered with ventral epithelium.

Figs. 19-23, grafts in posterior prepharyngeal region. Fig. 19, normal anteroposterior, reversed dorsoventral orientation, union incomplete. Fig. 20, normal orientation, union complete, graft head covered with dorsal epithelium. Figs. 21 and 22, normal orientation, union incomplete, lateral and dorsal views of same graft. Fig. 23, normal orientation, union incomplete, graft head and outgrowth ventral.

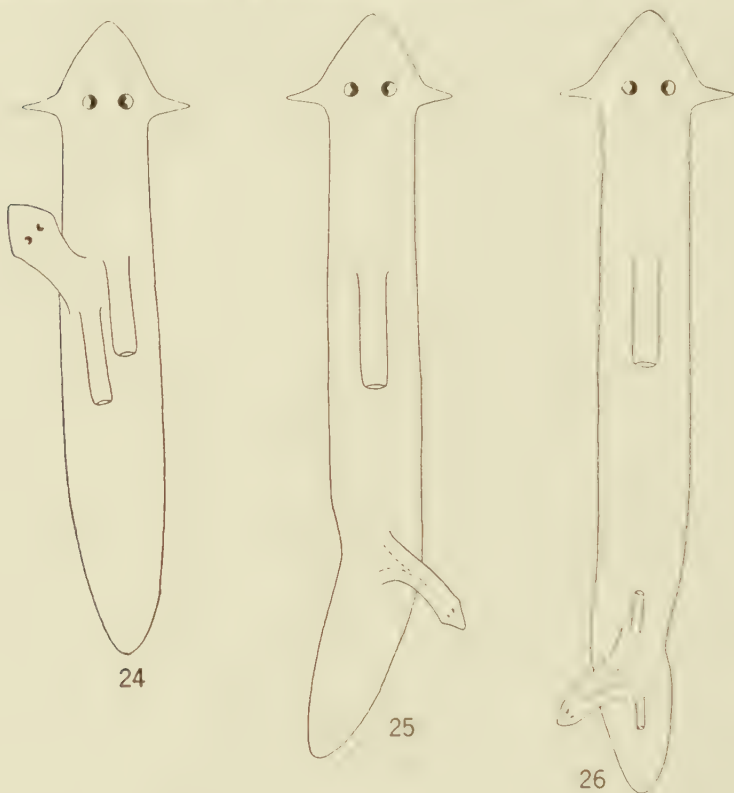
region from the host body and the development of a secondary pharynx slightly posterior to that of the host. Reorganization of the gut in relation to the induced pharynx has also taken place but is not shown in the figure.

The general results obtained with homoplastic grafts of the ganglionic region of *P. dorocephala* into the postpharyngeal region are given in Series 5 and 6 of Table I. Series 5 consists of cases of ganglionic grafts into the middle postpharyngeal region without subsequent removal of the anterior end of the host; and Series 6, of cases of ganglionic grafts into the middle and posterior postpharyngeal region with subsequent removal of the anterior end of the host at some level anterior to the graft. In Series 5 the usual result is some degree of head development and induction of a postcephalic outgrowth from the body of the host (Fig. 25). In these cases the induced outgrowth unquestionably represents a new polarity, determined by the graft; but there is no indication of reversal of polarity in other parts of the host body, such as occurs in Series 6. In general, such reversal of polarity occurs much more frequently when the anterior end of the host is removed after the graft and outgrowth have developed; but in a few cases, which are not included in the tabulated data, reversal of polarity did occur without removal of the anterior end of the host. A case of this sort is shown in Figure 26. Here the graft has induced a postcephalic outgrowth and the development of two pharynges, one anterior to the graft and in reversed position, the other posterior to the graft and in normal position. The gut (not shown in the figure) is reorganized in relation to the two pharynges. In this case the graft has induced reorganization in the host body for some distance anterior and posterior from the level of implantation, while in the more anterior levels the original organization of the host body remains unchanged.

As Series 6, Table I, shows, numerous cases of reversal of polarity in the postpharyngeal region of the host body have resulted from implantation of the ganglionic region into postpharyngeal levels, with subsequent removal of the anterior end of the host. Figures 27 and 28 show cases of this sort. In both of these cases the head which has developed from the graft has become the dominant region and functionally the anterior end.



In some cases of homoplastic ganglionic grafts in the extreme posterior postpharyngeal region of *P. dorocephala* development of a head and induction of a postcephalic outgrowth occurred, but no



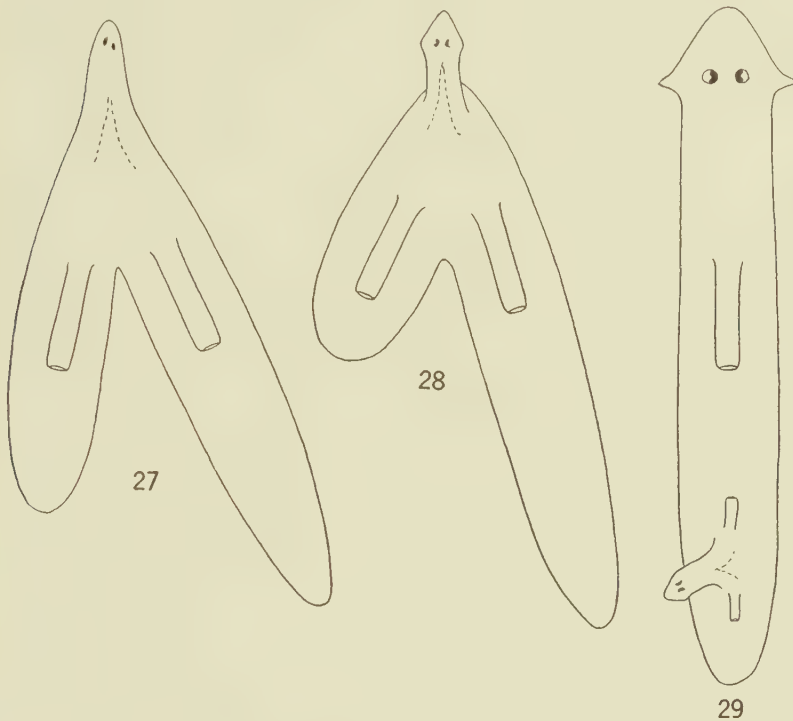
FIGS. 24-26.—*Planaria dorocephala*. Triangular, homoplastic ganglionic grafts in pharyngeal and postpharyngeal regions.

Fig. 24, graft in pharyngeal region, union incomplete, head normal. Graft has induced postcephalic outgrowth from host body and new pharynx in host body.

Fig. 25, graft in postpharyngeal region in reversed anteroposterior, normal dorsoventral orientation, union incomplete, graft head with both dorsal and ventral epithelium, induced postcephalic outgrowth with dorsal epithelium external, ventral epithelium in invagination.

Fig. 26, graft in postpharyngeal region in reversed anteroposterior, normal dorsoventral orientation, union incomplete, graft head with dorsal and ventral epithelium, induced postcephalic outgrowth with dorsal epithelium external, ventral epithelium in invagination. The graft head has also induced development of two pharynges in host body, one in normal, one in reversed polar orientation.

visible reversal of polarity anterior to the graft level took place—that is, no pharynx developed during the period of observation.



FIGS. 27-29.—Triangular homoplastic ganglionic grafts in postpharyngeal region in normal orientation. Figs. 27 and 28, *Planaria dorocephala*. Fig. 29, *P. maculata*.

Fig. 27, union complete, head and postcephalic outgrowth covered with dorsal epithelium. Graft head has induced development of two pharynges in opposite polar orientation in host body. Anterior end of host removed posterior to pharynx after development of graft and development of new head prevented by graft and polarity of anterior portion of host body reversed (left side of figure).

Fig. 28, a case similar to Fig. 27 except that union is incomplete and graft head is normal.

Fig. 29, graft in posterior postpharyngeal region, union incomplete, head with dorsal and ventral epithelium; induced postcephalic outgrowth with dorsal epithelium external. The graft head has induced postcephalic outgrowth from the host body and also development of two pharynges in opposite orientation in host body. Anterior end of host was not removed.

These cases, however, were among the earlier experiments and were kept under observation for only about four weeks. Later experi-

ments have shown that reversal of polarity by the graft often does not become evident in so short a time. It is probable, therefore, that in at least some of these cases reversal of polarity anterior to the graft would have taken place if the animals had been kept for a longer time.

It will be observed from the figures that the length of the postcephalic outgrowth and the effect of the graft in inducing reorganization in the host body differ in different cases at the same level of the body. This difference is most clearly evident in grafts in the postpharyngeal region. In some of the cases described and figured above, the grafts into the postpharyngeal region develop a head and induce a postcephalic outgrowth but do not induce development of a pharynx or pharynges and reorganization of the gut in the host body (Fig. 25, also Santos, 1929, Fig. 22). In other cases development of one or two pharynges and corresponding reorganization of the gut in the host body are induced by the graft (Figs. 26-28). These differences are perhaps due in part to differences in size of the graft, in its degree of union with the host tissues, or in its physiological condition in relation to that of the host. It is also possible that in some cases the grafted animals were not kept under observation long enough for complete development of the effect of the graft. The induced development of new pharynges in the host body occurs rather slowly, in most cases requiring several weeks. In all cases the grafted animals remained under observation for at least a month, and often for three or four months. Many of them were finally fixed for histological examination, and it is possible that in some cases further-induced reorganization in the host body might have occurred if the animals had been kept for a longer time. In most of the later experiments the animals were kept until it appeared certain that no further development would occur.

Certain characteristics of the heads which develop from the grafts and of the induced postcephalic outgrowths require some further consideration. The form of the graft head ranges from normal with cephalic lobes through various abnormal forms to bluntly pointed or rounded head regions more or less conical in form with a single eye. The degree of healing of the graft into the host body is an important factor in determining these differences in head form. For



example, some portion of the cut surface of the graft may fail to unite with the host tissues. Under these conditions this part of the graft heals like any other cut surface, and the dorsal and ventral epithelium of the graft unite with each other. In such cases the head which develops shows the characteristic dorsoventral difference in pigmentation and appearance of dorsal and ventral epithelium. Heads of this sort usually develop cephalic lobes and may be completely normal (Figs. 4, 5, 6, 9, 10, 13, 14, 17, 19, 22, 23, 24, 26, 28).

When the piece is grafted with normal dorsoventral orientation and the graft unites completely with the tissue of the host, dorsal epithelium of the graft with dorsal epithelium of the host and ventral epithelium with ventral, the graft head is rounded or bluntly pointed anteriorly and more or less conical in form, and is completely covered with the epithelium characteristic of the surface from which it grows out. A part of this epithelium belongs to the graft; a part, to the host. If it develops on the dorsal surface of the host, it is covered with dorsal epithelium (Figs. 7, 8, 10, 11, 12, 16, 27); if from the ventral surface, with ventral epithelium (Figs. 15, 18). So far as can be determined, no transformation of dorsal epithelium into ventral or of ventral epithelium into dorsal takes place. Such heads do not develop cephalic lobes and usually possess only a single eye, which may be elongated or otherwise abnormal in form. These facts suggest that union of dorsal and ventral epithelium of the graft is one of the necessary conditions for the development of the cephalic lobes.

When the graft is implanted with reversed dorsoventral orientation, the union with the host tissues is often less complete than with normal dorsoventral orientation, and the graft head possesses both dorsal and ventral epithelium but reversed in position with respect to the host (Figs. 4, 5, 6, 13, 14, 19).

In short, it appears from the facts that grafts of the ganglionic region retain their dorsoventrality but that in the cases of complete union of graft and host, that is, of dorsal with dorsal and ventral with ventral, the graft head does not develop both dorsal and ventral epithelium but is covered with the epithelium of the body surface from which it grows out.

As regards persistence of the polarity of the graft, the facts are not

so clear. In cases with reversed dorsoventral and anteroposterior orientation, the original polarity persists (Fig. 14); but in many other cases, particularly those in which the graft head is merely a rounded outgrowth from the dorsal or ventral surface of the host, it is impossible to determine whether or not the original polarity persists in the graft, for there is no indication of it in the form of the head. In the case of Figure 4 the five pointed regions may be anterior head regions; and if they are, they indicate a multipolar condition at least as regards the head tip.

The postcephalic outgrowth determined by the graft differs in certain respects from a normal postcephalic region. It is very commonly more or less cylindrical instead of flattened. If it develops from the dorsal surface of the host, it is covered on all sides with dorsal epithelium (Figs. 7, 8, 10, 13, 14, 16, 17, 19, 20, 21, 22, 24, 25, 26, 27, 28); and if it develops from the ventral surface, it is covered with ventral epithelium (Figs. 15, 18, 23). In all cases when the union between the graft and host is complete, and in many cases when it is not complete, a depression or invagination appears on the side of the host body opposite to that on which the outgrowth develops and at the same level as the outgrowth. As elongation of the outgrowth takes place, this depression may extend as a tubular invagination partly or completely through the body of the host and sometimes a greater or less distance into the induced outgrowth, in some cases all the way to the graft head. This characteristic of the induced outgrowth ranges, then, from a mere depression or concavity on the surface opposite the graft to an elongated tubular invagination extending the whole length of the outgrowth. In the figures of cases in which it is present, it is shown either as a depression in the surface (Figs. 12-15, 19-21) or by dotted lines when indicated as inside the induced outgrowth (Figs. 7, 8, 10, 16, 18, 20, 21, 22, 25, 26, 27, 28). When the outgrowth develops from the dorsal surface of the host, this invagination is lined with ventral epithelium (Figs. 7, 8, 10, 12, 16, 18, 20, 21, 22, 23, 25, 26, 27, 28), which apparently, however, becomes somewhat modified in the deeper regions of the more elongated invaginations. When the outgrowth develops from the ventral surface of the host, the invagination is lined with dorsal epithelium (Figs. 15, 23).

In short, the induced postcephalic outgrowth may be tubular in form with dorsal epithelium on the outer and ventral epithelium on the inner surface, or vice versa. It cannot then be regarded as a normal postcephalic region, but the fact that in the grafts into postpharyngeal levels new pharynges and postpharyngeal regions are determined in relation to it indicates that it is physiologically a postcephalic region. Likewise, the fact that the graft head may dominate the host body and control its motor activity through the induced outgrowth points to the conclusion that the outgrowth functions as a postcephalic region. Further histological data concerning the graft head and the induced outgrowth will appear in a later paper.

*Homoplastic grafts of the ganglionic region of Planaria maculata.*—The number of homoplastic grafts of the ganglionic region of *Planaria maculata* which have been made is not as large as in the case of *P. dorocephala*. Since the results obtained in the two species are essentially similar, tabulation and extended description of cases is regarded as unnecessary. In *P. maculata* the development of a head from the graft and the induction of a postcephalic outgrowth from the host body occur as in *P. dorocephala*, and the various head forms and their relation to the degree of union between graft and host are similar in the two species. The development of a depression or tubular invagination on the surface of the host body opposite the graft is also of frequent occurrence in *P. maculata* as in *P. dorocephala*. Two cases of homoplastic grafts of the ganglionic region into the postpharyngeal region of *P. maculata* are described and figured in the earlier paper (Santos, 1929, Figs. 25, 27), and a third similar case is shown in Figure 29 of the present paper. In all three of these cases the graft developed a head, induced a postcephalic outgrowth from the host body, and also determined the development of two pharynges and corresponding reorganization of the gut in the host body. One of the pharynges is anterior to the level of the graft and in reversed position with relation to the original polar axis of the host. The other is posterior to the graft level and in normal position with relation to the host axis (Fig. 29). In this case, as in similar cases in *P. dorocephala*, the graft head possesses both dorsal and ventral epithelium and is normal in form with cephalic lobes while the induced postcephalic outgrowth is entirely covered on its surface



with dorsal epithelium but shows an invagination lined with ventral epithelium from the ventral surface of the host.

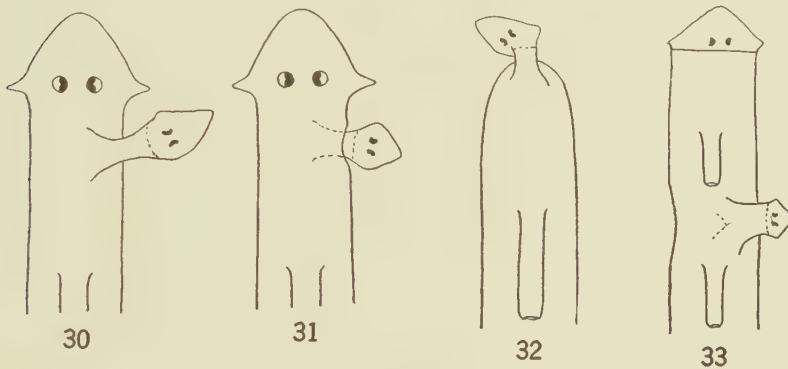
*Heteroplastic grafts of the ganglionic region between Planaria dorotocephala and P. maculata.*—More than one hundred heteroplastic grafts of the ganglionic region between *Planaria dorotocephala* and *P. maculata* have been made, both species serving both as donor and as host. The results are similar to those obtained with the homoplastic grafts in the two species. The point of chief importance with respect to the heteroplastic grafts is that the ganglionic region of one species is able to induce a postcephalic outgrowth from the body of the other species and, when implanted into the postpharyngeal region, to induce development of one or more pharynges and reorganization of the gut in the body of the host species. In other words, the physiological effect of the graft on the body of the host is not species-specific.

The data obtained, however, indicate one important difference between the two species. In general, grafts of the ganglionic region of *P. dorotocephala* seem to be more effective in inducing postcephalic outgrowth and, in the postpharyngeal region, the development of new pharynges and reorganization of the gut in the body of *P. maculata* than the ganglionic grafts of *P. maculata* into *P. dorotocephala*. With the ganglionic grafts of *P. dorotocephala* the induction of development in the body of *P. maculata* occurs more frequently and more rapidly than in the reverse case. Similarly, with small grafts representing a part of the ganglionic region resorption occurs less frequently when the graft is from *P. dorotocephala* than when it is from *P. maculata*.

A number of cases of heteroplastic ganglionic grafts between these two species have already been figured and briefly described in an earlier paper (Santos, 1926). In that paper, Figures 9, 13–15, 21, 23, 24, 26, 28, show cases of heteroplastic ganglionic grafts between *P. dorotocephala* and *P. maculata*. A few of these cases are more fully described in the present paper together with some cases not included in the earlier paper.

Since the results obtained with heteroplastic ganglionic grafts are similar to those described above for homoplastic grafts, and since figures and descriptions of cases of heteroplastic grafting have been

given in the earlier paper, only a few characteristic cases need be described here. In Figure 30 a case of implantation of the ganglionic region of *P. dorocephala* into the anterior postpharyngeal region of *P. maculata* is shown. The *P. dorocephala* head possesses both dorsal and ventral epithelium of *P. dorocephala* and is normal in form. The induced postcephalic outgrowth has developed from the dorsal surface of the host and is carried with the dorsal



FIGS. 30-33.—Triangular heteroplastic ganglionic grafts in prepharyngeal and pharyngeal regions.

Figs. 30 and 31, grafts of *Planaria dorocephala* in *P. maculata* in normal orientation, union incomplete, head with dorsal and ventral epithelium of donor. Fig. 30, graft head dorsal on host; induced postcephalic outgrowth covered with dorsal epithelium of host. Fig. 31, graft head ventral on host; induced postcephalic outgrowth covered with ventral epithelium of host.

Figs. 32 and 33, grafts of *P. maculata* in *P. dorocephala*. Fig. 32, graft in anterior prepharyngeal region, normal orientation, union incomplete, graft head with dorsal and ventral epithelium of donor, induced postcephalic outgrowth covered with dorsal epithelium of host. Anterior end of host removed after development of graft, and graft head has prevented development of a new head on host after the second removal. Fig. 33, graft in pharyngeal region, reversed anteroposterior, normal dorsoventral orientation, union incomplete, graft head with dorsal and ventral epithelium of donor, induced postcephalic outgrowth covered with dorsal epithelium of host. The graft head has induced development of a pharynx posterior to the graft level and the host has reconstituted a pharynx anterior to the graft level. Anterior end of host removed after development of graft and new normal head developed.

epithelium characteristic of *P. maculata*. In this case there is no invagination on the ventral surface of the host body. Figure 31 shows a case of *P. dorocephala* graft in *P. maculata* at the same body level

as Figure 30. In this case, however, the head and the induced outgrowth developed on the ventral side of the host body. The head is normal in form and possesses both the dorsal and ventral epithelium of *P. dorotocephala*, while the induced outgrowth is covered with the ventral epithelium of *P. maculata*. No invagination from the dorsal surface of the host has developed. In Figure 32 (Santos, 1929, Fig. 9), which shows a ganglionic graft from *P. maculata* implanted in the prepharyngeal region of *P. dorotocephala* at the same level as Figures 30 and 31, the anterior end of the host was removed after development of the graft head, and a new head developed. After this second removal at a level just anterior to the graft, development of the host head was completely inhibited, and the graft head functioned as the head of the animal. Other cases of implantation of the ganglionic region of *P. dorotocephala* into *P. maculata* are shown in Figures 13-15 of the earlier paper (Santos, 1929). Figure 13 of the earlier paper is similar to Figure 30 described above. Figure 14 of the earlier paper is a case with reversed dorsoventral orientation of the graft and is similar to the homoplastic graft shown in Figure 13 of the present paper. Figure 15 of the earlier paper is a case with reversed dorsoventral and anteroposterior orientation of the graft similar to the homoplastic graft in Figure 14 of the present paper. Other cases of successful heteroplastic ganglionic grafts in the prepharyngeal region differ from the homoplastic grafts only in the fact that the graft head possesses the epithelium and, when fully developed, the form characteristic of the donor species, while the induced outgrowth develops from the host species and its outer surface is covered with epithelium characteristic of the surface of the host species. Also, in case an invagination from the opposite surface of the host body occurs, this is lined with epithelium characteristic of that surface of the host species.

In Figure 33 a graft of the ganglionic region of *P. maculata* into the pharyngeal region of *P. dorotocephala* is shown. The graft head is a normal *P. maculata* head, and the postcephalic outgrowth from the dorsal surface of the host is covered with dorsal *P. dorotocephala* epithelium. In this case the pharyngeal region and the head of the host were removed. A new normal head has developed at the anterior cut end of the host body, and a new pharynx, in normal posi-

tion anterior to the graft level. The development of this pharynx is undoubtedly determined by the new dominant head region at the anterior end of the host body, not by the graft head. Posterior to the level of the graft another pharynx, evidently determined by the graft head, has developed. Here the *P. maculata* graft head has had no visible effect on levels anterior to it but has determined reorganization at more posterior levels of the *P. dorotocephala* body.

The heteroplastic ganglionic grafts at postpharyngeal levels are of greater interest than the prepharyngeal because, as in the homoplastic grafts, they induce more extensive reorganization in the host body than grafts at more anterior levels. In Table II numerical

TABLE II

HETEROPLASTIC GRAFTS OF GANGLIONIC REGION BETWEEN *Planaria dorotocephala*  
AND *Planaria maculata*; LENGTH, 10-22 MM.

All grafts were triangular and included approximately the whole ganglionic region, and all were implanted in the postpharyngeal region of the host.

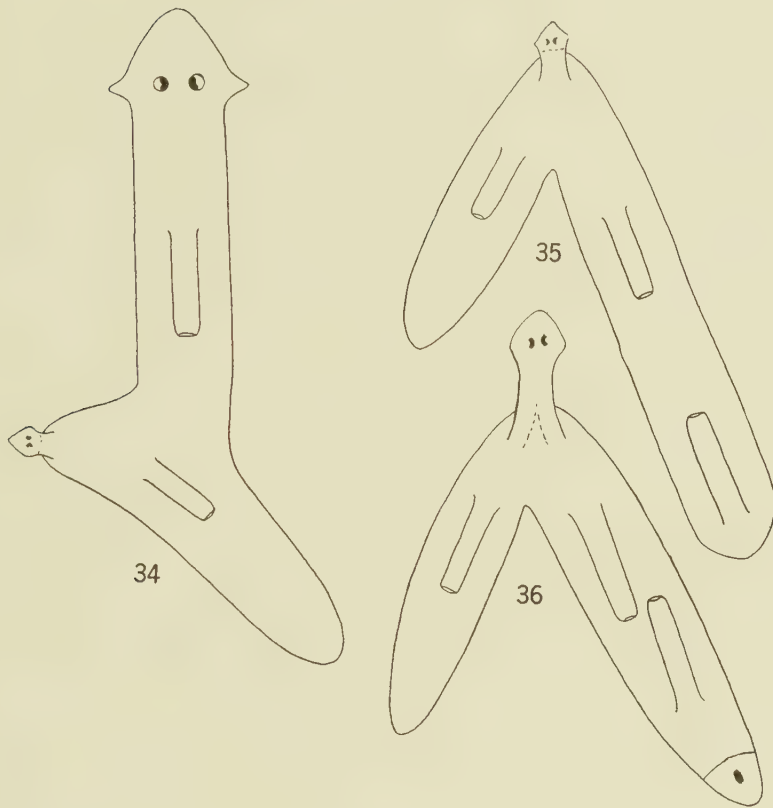
| Series and Species of Host           | Number of "Takes" | Controls ("Non-Takes") | Induction of Outgrowth | Anterior End of Host Removed     | Reconstitution of New Head Inhibited | Reversal of Polarity |
|--------------------------------------|-------------------|------------------------|------------------------|----------------------------------|--------------------------------------|----------------------|
| 1. <i>Planaria dorotocephala</i>     | 24                | 33                     | 24                     | .....                            | .....                                | .....                |
| 2. <i>P. dorotocephala</i> . . . . . | 3                 | 17                     | 3                      | 3 (fission posterior to pharynx) | 3                                    | .....                |
| 3. <i>P. dorotocephala</i> . . . . . | 3                 | 1                      | 3                      | 3                                | 2                                    | .....                |
| 4. <i>P. maculata</i> . . . . .      | 10                | 2                      | 10                     | 4                                | .....                                | 4                    |
| 5. <i>P. maculata</i> . . . . .      | 5                 | 5                      | 5                      | 5                                | 5                                    | 5                    |
| 6. <i>P. maculata</i> . . . . .      | 19                | 3                      | 19                     | .....                            | 19                                   | 19                   |

data are given for the most successful series of such grafts. Series in which most of the grafts failed to unite with the host tissue or were resorbed are not included in the table. In Series 1, 2, 3, *P. dorotocephala* is host and *P. maculata* donor; in Series 4-6, *P. maculata* is host and *P. dorotocephala* donor. The table shows that in all "takes" induction of an outgrowth from the host body occurred. In the cases in which *P. dorotocephala* was host (Series 1, 2, and 3) there was, however, no reversal of polarity in the host body. In the three cases of Series 2 and in the two cases of Series 3 the anterior end of the host was removed posterior to the pharynx after the graft head and outgrowth developed, and the graft head prevented development of a



new head from the anterior cut surface of the host body. In Series 4-6, with *P. maculata* as host, the anterior end of the host was removed in all cases after the graft head and induced outgrowth developed. As in the case of similar homoplastic grafts, a new head, either normal or more or less inhibited in form, developed on the anterior end of the host after this first removal. This head was then removed, and in some cases a head developed again but more inhibited in form than the first, while in other cases no head developed. In cases in which the second head did develop, it was also removed; and after this second removal of the reconstituted head, further head development at the anterior end of the host might be completely prevented and the anterior end might be transformed into a posterior end. Here, as in the homoplastic grafts, the dominance of the graft head evidently extends gradually in the anterior direction to the anterior cut end of the host body; and, even though it does not completely inhibit reconstitution of a head at first, it may do so after a second or third removal of the head and may finally reorganize that portion of the host body anterior to the graft level as a posterior end. The nearer the level of removal of the anterior end of the host to the level of the graft and the more nearly normal the graft head, the sooner does complete inhibition of development of a new host head, and reorganization of the anterior portion of the host body into a posterior end, occur. The last two columns of Table II give only the final results as regards inhibition of development of the host head and reversal of polarity in the host body anterior to the graft level.

A few characteristic cases are selected for description. In Figure 34 (Santos, 1929, Fig. 21) a case of *P. dorotocephala* graft into the anterior postpharyngeal region of *P. maculata* is shown. The graft head is normal, and the induced postcephalic outgrowth from the host body is short; but the host body is drawn out laterally in the region of the graft head, into a broad blunt extension. To what extent this change in form of the host body represents growth and to what extent deformation is uncertain. It developed gradually, apparently in relation to the mechanical tension exerted by the graft head in its efforts to advance. Reorganization in the case of Figure 34 has been induced only posterior to the level of the graft, and there



FIGS. 34-35.—Triangular, heteroplastic ganglionic grafts of *Planaria dorocephala* in postpharyngeal region of *P. maculata*. Union incomplete, graft heads with dorsal and ventral epithelium of donor, induced postcephalic outgrowth covered with dorsal epithelium of host.

Fig. 34, graft in normal orientation, induction of short postcephalic outgrowth, lateral extension of host body, and new pharynx posterior to graft level.

Fig. 35, graft in reversed anteroposterior, normal dorsoventral orientation. Graft has induced postcephalic outgrowth and two new pharynges, one posterior to graft level in normal polar orientation (left), the other anterior to graft level in reversed polar orientation (right). After development of graft, anterior end of host was removed posterior to host pharynx. A new head and pharynx developed. Head was removed, new head again developed; but after removal of this, development of head was prevented by graft (lower right in figure).

FIG. 36.—Graft in reversed anteroposterior, normal dorsoventral orientation. Induction as in Fig. 35. Anterior end of host removed twice; second reconstituted head partially inhibited by graft (lower right in figure). *Planaria maculata* triangular, ganglionic graft in *P. dorocephala* body.

is no reversal of polarity at more anterior levels. The graft was made at about the level of fission, so that the region anterior to it is a part of the first zooid and under the dominance of the host head. This fact probably accounts for the absence of induced reorganization anterior to the graft levels. Both the homoplastic ganglionic grafts in the postpharyngeal region already described and similar heteroplastic grafts to be described below show that at more posterior postpharyngeal levels (that is, well within the posterior zooid region of the host which is more or less physiologically isolated from the dominance of the head) reorganization anterior as well as posterior to the graft level may occur.

In the case of Figure 35, a ganglionic graft from *P. dorocephala* near the middle of the postpharyngeal region of *P. maculata*, the graft has developed a *P. dorocephala* head and induced post-cephalic outgrowth covered with dorsal epithelium from the *P. maculata* body. The host body has become bent upon itself at the level of the graft apparently in consequence of locomotion with the graft head in advance. The anterior end of the host body is on the right side of the figure. Development of a pharynx and corresponding reorganization of the gut has taken place both posterior and anterior to the graft level, representing in the latter case a reversal of polarity with pharynx in reversed position. In this case the head of the host was removed when the graft was made, and a new head developed. The anterior end was again removed after the graft head had developed and reorganization in the host body had taken place. After this removal no head developed at the anterior end of the host, although the persistence of the host pharynx indicates that polarity has not been completely reversed in this region. Apparently, the graft head has inhibited head development at the anterior end of the host body even though the level of the cut surface is at a considerable distance anterior to the graft.

Figure 36 shows a case very similar to Figure 35, but with a *P. maculata* graft in a *P. dorocephala* body. The graft head has induced reorganization in the host body anterior and posterior to its level. The anterior end of the host was cut off in the pharyngeal region, and a new normal head and pharynx developed. This head was removed; and the second reconstituted head, as shown in Figure

36, was teratomorphic, i.e., partially inhibited. Further removal was not made in this case.

In the case shown in Figure 37 (Santos, 1929, Fig. 26) the *P. maculata* graft is implanted at a more posterior level of the postpharyngeal region of *P. dorocephala*; and reorganization and pharynx development occur both posterior and anterior to the graft level, even though the head of the host is present. The level of the graft in this case is well within the posterior zooid region, and the presence of the host head does not prevent reversal of polarity anterior to the graft level.

In Figure 38 the *P. dorocephala* graft developed a head and induced development of a postcephalic outgrowth from the *P. maculata* body but did not determine further visible reorganization within the period of observation, which in this case was 34 days. Further reorganization might have occurred later. In Figure 39 (Santos, 1929, Fig. 29), a *P. maculata* graft in *P. dorocephala*, a graft head and induced host outgrowth appear, and a small pharynx has developed just posterior to the level of the induced outgrowth.

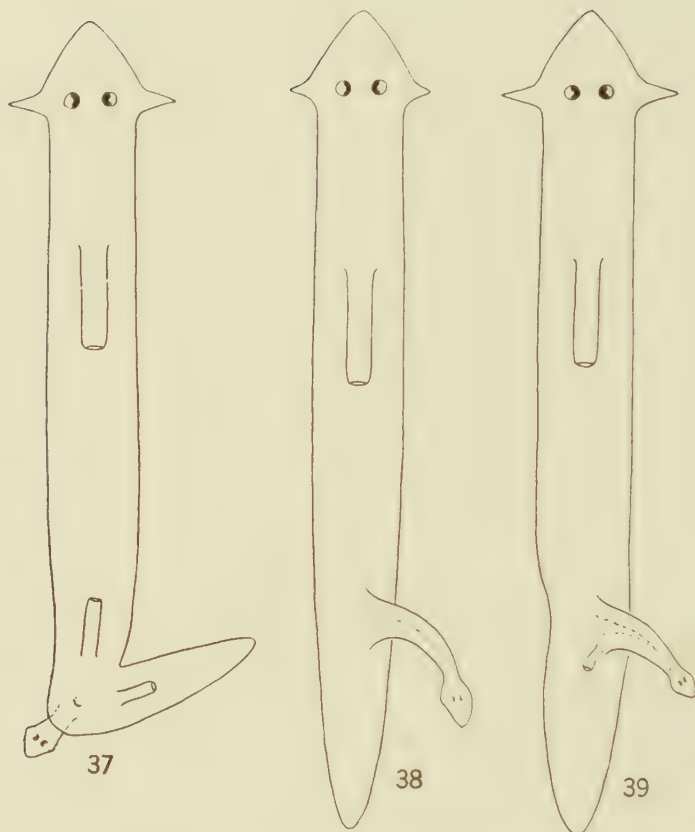
In the case shown in Figure 40 (Santos, 1929, Fig. 28) the *P. maculata* graft was implanted in the extreme posterior postpharyngeal region of *P. dorocephala*. The graft head induced development of a postcephalic outgrowth and reversal of polarity in the host body for a considerable distance anterior to its level, as indicated by the development of a pharynx in reversed position. The dotted outline at the right in Figure 40 indicates the position assumed by the graft head and the region of reversed polarity during forward locomotion.

In the figures of heteroplastic grafts of the ganglionic region given in the present paper the boundary between the epithelium of the graft head and that of the induced postcephalic outgrowth is approximately indicated, but the difference in pigmentation characteristic of the two species which is clearly evident in the living animals is not shown. Figures showing this difference in pigmentation will be given in connection with the histological data.

#### GRAFTS FROM POSTCEPHALIC REGIONS

The data concerning grafts of pieces from postcephalic regions are less complete than those concerning ganglionic grafts. It became





FIGS. 37-39.—Triangular, heteroplastic ganglionic grafts in postpharyngeal region in normal orientation, union incomplete, graft heads with dorsal and ventral epithelium of donor.

Fig. 37, graft of *Planaria maculata* in *P. dorocephala*. Graft head on ventral side of host. Induced postcephalic outgrowth covered with ventral epithelium of host. Graft has induced development of two pharynges in host body, one posterior to level of graft in normal orientation, one anterior to level of graft in reversed polar orientation.

Fig. 38, graft of *P. dorocephala* in *P. maculata*. Induced postcephalic outgrowth covered externally with dorsal epithelium of host; ventral invagination lined with ventral epithelium.

Fig. 39, graft of *P. maculata* in *P. dorocephala*. Induced postcephalic outgrowth covered externally with dorsal epithelium of host; ventral invagination lined with ventral epithelium. Graft has induced development of one small pharynx just posterior to graft level.

evident early in the course of the work that the ganglionic grafts were of greater interest in many respects than the postcephalic grafts; consequently it seemed desirable to obtain, first of all, fairly complete data concerning them. A large number of grafts from prepharyngeal, pharyngeal, and postpharyngeal levels of the donors into prepharyngeal and pharyngeal regions of the host have been made; but the results of grafting postcephalic pieces into postpharyngeal regions have not yet been determined. Up to the present, also, most of the grafts of postcephalic pieces have been homoplastic, and in *P. dorocephala*. Further experiments along these lines are planned for the near future.

Data concerning postcephalic grafts are presented here chiefly for the purpose of showing some of the differences between these and the ganglionic grafts.

*Homoplastic grafts of pieces from the prepharyngeal region.*—In all except a few of the earlier experi-

ments the pieces grafted were in the form of isosceles triangles. In some cases the base of the triangular piece grafted represented almost the whole

width of the body and was either anterior or posterior (Fig. 41). In other cases the triangular piece was taken from one side of the body, the base repre-

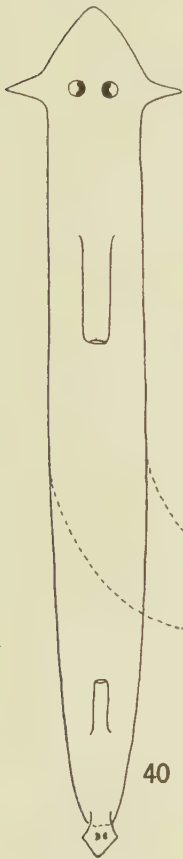
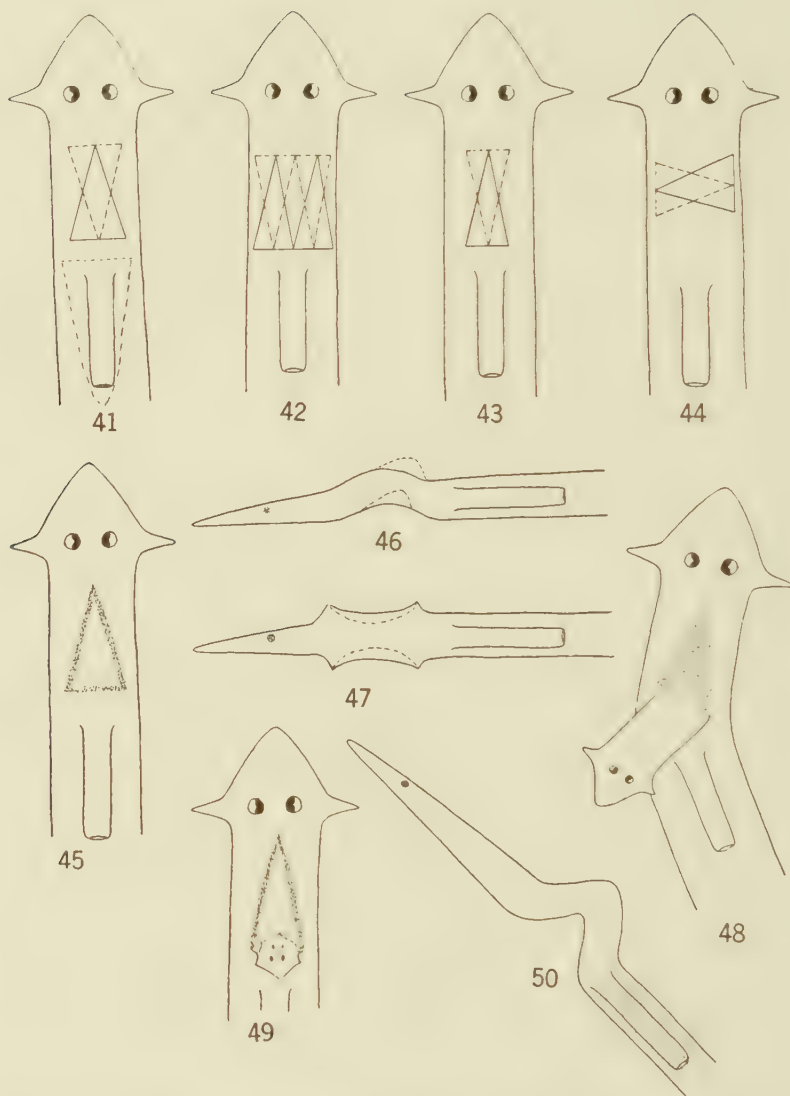


FIG. 40.—Triangular heteroplastic ganglionic graft of *Planaria maculata* at posterior end of body of *P. dorocephala* in reversed anteroposterior, normal dorsoventral orientation. Union incom-

plete; graft head with dorsal and ventral epithelium of donor; induced postcephalic outgrowth covered with dorsal epithelium of host. Graft has induced development of new pharynx in reversed polar orientation in body of host.

senting slightly less than one-half the body width and being either anterior or posterior (Fig. 42), and was implanted in the median region (Fig. 43). In still other cases the grafts were cut, as in Figure 44, and grafted with the base of the triangle either anterior or posterior on the host body (Fig. 41). The experiments do not cover all the possible orientations of graft in relation to the host, but



FIGS. 41-50.—Homoplastic grafts of triangular pieces from prepharyngeal region of *Planaria dorotocephala*.

Figs. 41-44, to show the region of body, shape, size, orientations and levels of implantation of triangular pieces used as grafts from prepharyngeal region. Pieces with bases posterior (Figs. 41-43) or toward right (Fig. 44) drawn in solid lines; pieces with bases anterior (Figs. 41-43) or toward left (Fig. 44) drawn in broken lines. The triangu-

lar outlines in Fig. 41 also indicate approximately the level of implantation of grafts into the prepharyngeal and the pharyngeal regions.

Fig. 45, dorsal view of graft of prepharyngeal piece into prepharyngeal region in normal orientation. Union complete.

Fig. 46, lateral sectional view of prepharyngeal piece into prepharyngeal region in reversed anteroposterior, normal dorsoventral orientation. Union complete. Graft is incorporated with slight growth of new tissue along lines of union.

Fig. 47, lateral sectional view of prepharyngeal piece into prepharyngeal region in normal anteroposterior, reversed dorsoventral orientation. Union complete.

Fig. 48, dorsal view of graft of prepharyngeal piece into prepharyngeal region in reversed anteroposterior, normal dorsoventral orientation. Union incomplete. Graft head and postcephalic outgrowth both developed from graft and both normal, possessing dorsal and ventral epithelium. Graft has migrated posteriorly and original region of implantation is filled in with new tissue, indicated by shading.

Fig. 49, dorsal view of graft of prepharyngeal piece into prepharyngeal region in reversed anteroposterior, normal dorsoventral orientation. Union incomplete. Graft has developed a normal head from its anterior end, and the host has developed a normal head on its cut surface facing anteriorly at posterior end of implantation opening.

Fig. 50, lateral sectional view of graft of prepharyngeal piece into pharyngeal region. The graft is in normal orientation. The graft has migrated anteriorly, part of the original region of implantation is filled in with new tissue (indicated in the figure by shading), and new pharynx has developed in it.

grafts of prepharyngeal pieces into the same level of the host have been made in normal anteroposterior with normal or reversed dorsoventral orientation, in reversed anteroposterior with normal dorsoventral orientation; also, grafts of prepharyngeal pieces into the pharyngeal region with reversed anteroposterior and normal dorsoventral orientation have been made—more than three hundred cases of complete or partial union of graft and host in all; and in many cases subsequent operations were performed, chiefly for the purpose of determining the effect of orientation of the graft in the host body. It is impossible to present all the various results at this time, but some of the more important are briefly described.

Considering first the grafts of prepharyngeal pieces into approximately the same body level of the host as that from which the graft was taken, it is found that such grafts in normal orientation usually unite completely with the host body and are incorporated in it (Fig. 45). They may give rise at first to a slight dorsal elevation and ventral invagination never greater than that indicated by the unbroken lines in Figure 46, which gradually disappears and is often very slight or absent from the beginning.



Grafts with reversed anteroposterior and normal dorsoventral orientation which unite completely with the host body show a more pronounced and more persistent dorsal elevation (Fig. 46, dotted lines) than those in normal orientation, and a gradual change in position of the elevation in the posterior direction often occurs with the development of new tissue in the host body at the original level of implantation and anterior to the graft. In cases with normal anteroposterior and reversed dorsoventral orientation and with complete union, elevation occurs both dorsally and ventrally about the margins of the graft while the middle region is concave both dorsally and ventrally (Fig. 47). The marginal elevation probably indicates that more growth occurs along the line of union than with normal dorsoventral orientation (Fig. 46).

Grafts in reversed anteroposterior and either normal or reversed dorsoventral orientation show incomplete union more frequently than those with normal orientation. In most such cases observed, it was the anterior end of the graft which failed to unite, and a head developed from it. Figures 48 and 49 show cases of this sort. In the case of Figure 48 a normal head develops on the original anterior end of the graft, now directed posteriorly; and the tissue of the graft is gradually drawn out, apparently by the attachment and mechanical tension exerted by the head, and forms a normal post-cephalic region. The original position of the graft is largely occupied by new tissue, indicated in Figure 48 by shading. In the case of Figure 49 a head, directed posteriorly, develops from the original anterior end of the graft; and another, directed anteriorly and lying beneath the graft head, from the anterior cut surface of the hole in the host body. One case has been observed in which the posterior region of a grafted piece failed to unite and gave rise to a posterior end which developed on the ventral side of the host.

Some fifty grafts of prepharyngeal pieces into the pharyngeal region with complete or partial union have been made. In these cases a triangular piece including the whole pharyngeal region is removed from the host, and the triangular graft inserted in the hole thus made. Figure 50 indicates the usual result in cases of complete union in normal orientation. The region of the graft at first becomes dorsally elevated to a greater extent than in grafts at prepharyngeal

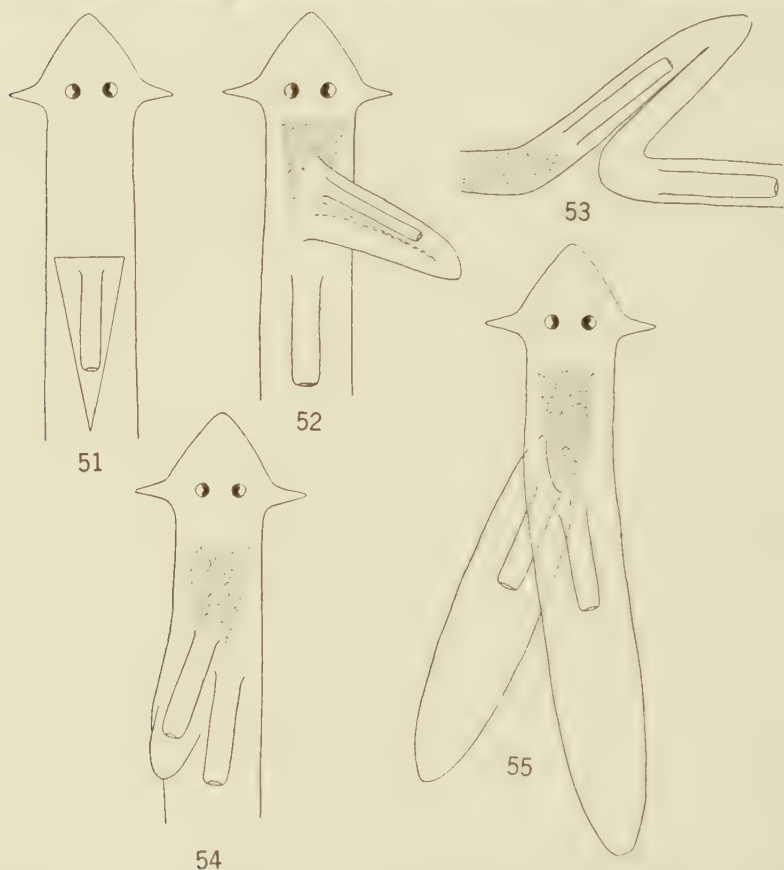
levels (Fig. 46), and a corresponding concavity appears on the ventral surface; but this distortion gradually disappears. Also, the graft appears to migrate in the anterior direction, and an area of new tissue develops posterior to it at the original level of implantation. In this area of new tissue posterior to the graft a new pharynx develops. This change in position of the graft evidently results from the difference in physiological condition at different levels of the body. In these cases a piece is implanted at a level posterior to its original level and gradually changes its position toward its original level. As will appear below, migrations either in the anterior or posterior direction occur in other cases. Discussion is postponed until these further cases have been described.

*Homoplastic grafts of pieces from the pharyngeal region.*—Pieces including the whole pharyngeal region with the base of the triangle anterior (Fig. 51) were transplanted to the prepharyngeal region with normal orientation. When healing is complete, such grafts give rise to an elongated dorsal elevation with a tubular invagination from the ventral surface (Figs. 52 and 53). The pharynx of the graft lies on the anterior side of this elevation, and the mouth opens into the ventral invagination near the apex of the elevation (Figs. 52 and 53). This position of the mouth, which was originally close to the posterior end of the graft, indicates that the posterior side of the dorsal elevation originates from the host tissue. This graft gradually migrates posteriorly toward the pharyngeal region of the host, that is, toward the body level corresponding to that from which the graft was taken. In Figure 54 another case is shown. Here the graft implanted at a level entirely anterior to the pharynx of the host has migrated so far posteriorly that the graft pharynx lies almost at the same level as the host pharynx but somewhat dorsal to it.

The case shown in Figure 55 is also a graft of the pharyngeal region into the prepharyngeal region but with incomplete union between graft and host and development of a posterior end containing the graft pharynx. This posterior end extends beneath a part of the lateral region of the host body but is entirely free from this part, so that an opening through the host body between the lateral strip and the new posterior end exists, as indicated in Figure 55.

Grafts of the pharyngeal region into the pharyngeal region have

been made only in reversed anteroposterior and normal dorsoneutral orientation. These grafts were cut as indicated in Figure 51 and



FIGS. 51-55.—Homoplastic grafts of triangular pieces from pharyngeal into pre-pharyngeal region in normal orientation in *Planaria dorotocephala*.

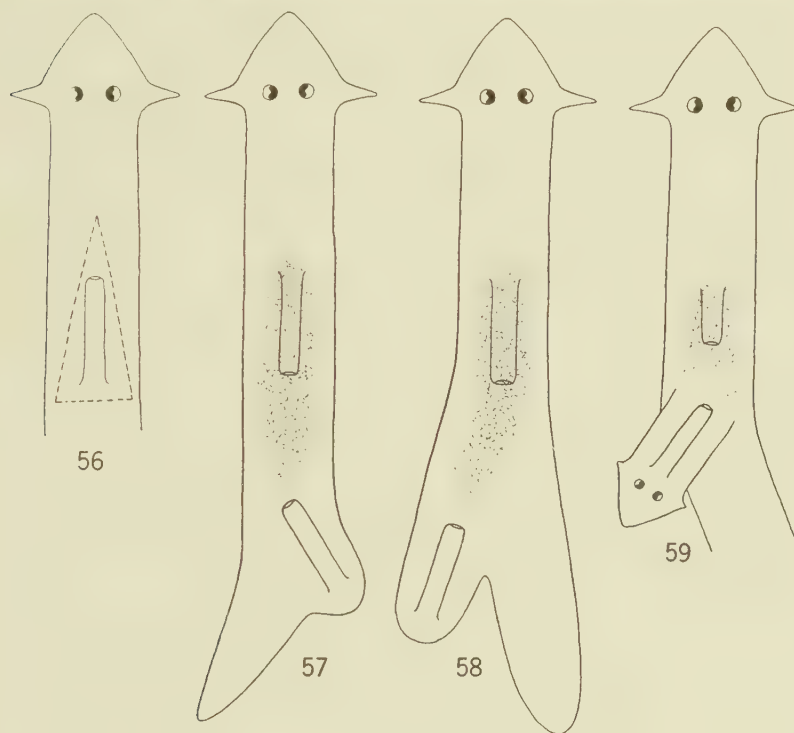
Fig. 51, the triangular outline indicates the piece used as graft.

Figs. 52 and 53, dorsal and lateral sectional views of same graft. Union complete. Graft has given rise to a dorsal elevation with corresponding ventral invagination and migrates posteriorly, the original region of implantation being filled in with new tissue, indicated by shading.

Fig. 54, dorsal view of another case in which the direction of migration is posterolateral, the original region of implantation being filled in with new tissue.

Fig. 55, dorsal view of another case of incomplete union. The graft has given rise to a new posterior end and has migrated posteriorly, the original region of implantation being filled in with new tissue.

implanted in the position indicated in Figure 56. Such grafts also develop a dorsal elevation and ventral invagination; but instead of remaining in the pharyngeal region in which they were implanted, they migrate posteriorly, and sooner or later approach one side or the other of the body so that the original dorsal elevation finally



FIGS. 56-59.—Homoplastic grafts of triangular pieces from the pharyngeal region into the pharyngeal region in reversed anteroposterior, normal dorsoventral orientation.

Fig. 56, the triangular outline shows the position of the graft after implantation.

Figs. 57 and 58, union complete. Grafts have migrated posteriorly; the original region of implantation is filled in with new tissue, and a new pharynx has developed in it.

Fig. 59, union incomplete. The graft has developed a normal head at its anterior end and a postcephalic region, and has migrated posteriorly, the original region of implantation being filled in with new tissue, indicated by shading.

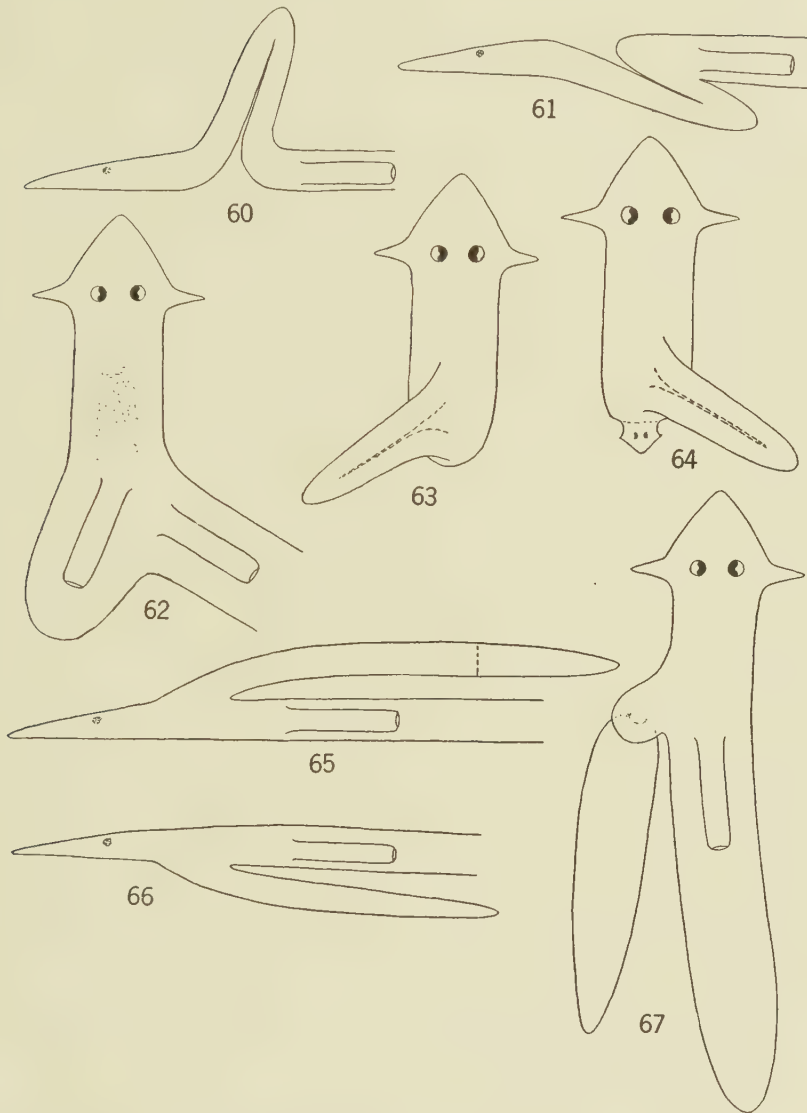
extends more or less posteriorly from a lateral margin of the body (Figs. 57 and 58). During this migration the ventral invagination gradually disappears; and when the condition of Figures 57 and 58



is attained, the dorsal side of the graft extension is covered with dorsal epithelium, the ventral side with ventral epithelium. The graft pharynx remains functional and is able to ingest food. In these cases the fact that the graft in reversed anteroposterior orientation does not remain at the body level corresponding to that from which it was taken, but migrates posteriorly, that is, with its anterior end in advance, is of particular interest since this migration results in bringing the graft to a body level far from the level from which it was taken.

Figure 59 shows another case of pharyngeal graft into the pharyngeal region with reversed anteroposterior and normal dorsoventral orientation. In this case, however, the anterior end of the graft failed to unite with the host tissue and gave rise to a normal head and a short prepharyngeal region developed from the graft tissue between the new head and the graft pharynx. In this case, also, the graft has migrated posteriorly and to a large extent out of the host body, and represents the prepharyngeal and pharyngeal regions of a new individual. In Figure 59 the new tissue anterior to the graft is indicated by shading.

*Homoplastic grafts of pieces from the postpharyngeal region.*—Sixty grafts from the posterior part of the postpharyngeal region into the prepharyngeal region with normal orientation gave complete union with the host. In such cases the graft region usually gives rise to an elongated elevation, which may be either dorsal or ventral, and a corresponding ventral or dorsal invagination (Figs. 60 and 61). In such cases it becomes impossible sooner or later to determine the exact boundaries of the graft, but apparently little or no migration occurs. In some cases, however, the dorsal elevation gradually migrates posteriorly and toward one side of the body, forming a lateroposterior extension (Fig. 62). Here the graft region develops a new pharynx, the ventral invagination disappears, and the final result is an apparently normal pharyngeal and postpharyngeal region formed in part from the graft and in part from the lateral region of the host body. This may become the chief posterior end of the individual and may undergo fission. In a number of these postpharyngeal grafts into the prepharyngeal region the posterior portion of the host body was cut off just posterior to the



FIGS. 60-67.—Homoplastic grafts of triangular pieces from the posterior post-pharyngeal region into the prepharyngeal region. *Planaria dorotocephala*.

Figs. 60 and 61, lateral sectional views showing dorsal or ventral elevation and corresponding ventral or dorsal invagination in cases of complete union in normal orientation.

Fig. 62, normal orientation, union complete. Graft at first formed a dorsal eleva-

tion. This migrated posteriorly and laterally; and as it reached the margin of the host body, ventral invagination disappeared, reorganization into a pharyngeal and postpharyngeal region took place, and gradual elongation followed in stages later than that shown in figure.

Fig. 63, normal orientation, union complete. After development of graft elevation, posterior end of host was removed just posterior to level of graft, and no regeneration occurred at the posterior cut surface.

Fig. 64, graft and subsequent operation as in Fig. 63. Posterior cut end of host body developed a normal head.

Fig. 65, normal orientation, union incomplete. Graft gave rise on dorsal side of host body to a posterior end which elongated and underwent fission at level indicated by broken line.

Fig. 66, normal anteroposterior, reversed dorsoventral orientation, union incomplete. Graft developed into a posterior region in reversed dorsoventral orientation with respect to host.

Fig. 67, normal orientation, union incomplete. Graft developed into a posterior region attached to ventral surface of extension of the host body.

elevation. In such cases there was no outgrowth of new tissue from the posterior cut surface of the host body to form a new posterior end; but the graft elevation gradually took the position of the posterior end, the ventral invagination disappeared, and a normal posterior region resulted, with development of a new pharynx either anterior to or in the anterior portion of the graft tissue. Meanwhile, gradual elongation of the whole body took place. Figure 63 represents an early stage in this process of reorganization. It shows the absence of regeneration of a posterior end by the host body, but the graft elevation has not yet undergone reorganization into a posterior end.

In three cases in which the posterior end of the host was removed just posterior to the graft, a normal head developed from the posterior cut surface (Fig. 64). The conditions concerned in this development of a head from the posterior cut surface are not known, but the possibility is suggested that the graft has cut off nervous connection between the head of the host and the posterior cut surface and so brought about a sufficient degree of physiological isolation of this region to permit a head to develop.

In all cases observed of incomplete union of postpharyngeal grafts into the prepharyngeal region, the posterior region of the graft has failed to unite and has given rise to a new posterior region, which

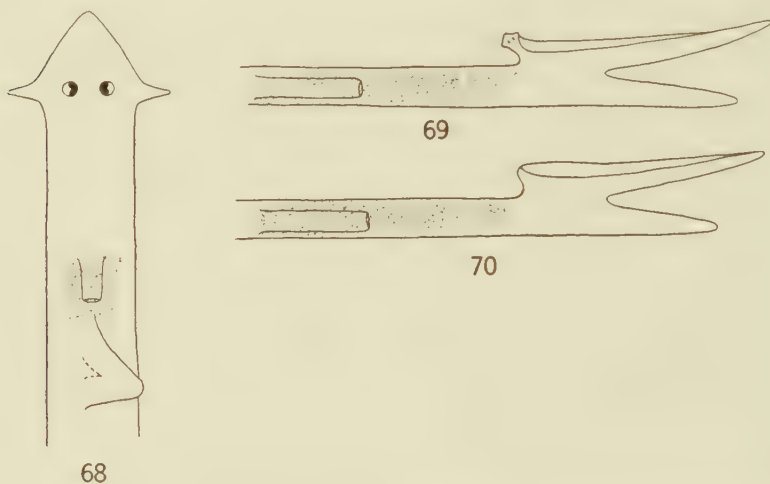
develops on either the dorsal or the ventral surface of the host and which may become as long as the host body (Figs. 65-67). In the case of Figure 67 the graft united with the host only at its anterior end, and the posterior outgrowth was somewhat to the left of the median line of the host. Here the graft finally came to lie entirely to the left of the host body and was connected with the host only by a slender peduncle; and the host body developed an extension originally ventral but gradually becoming lateral, apparently in consequence of the mechanical tension exerted by the outgrowth. These outgrowths function like normal posterior regions, and in the case of Figure 65 fission occurred at the level indicated by the dotted line in the figure; but unfortunately it was not determined whether they possessed pharynges. In these cases the elongation apparently results from growth of the graft, not from induction or reorganization in host tissues. This is indicated by the fact that in the case of Figure 65 the graft outgrowth arises from the dorsal surface of the host body but possesses, throughout its whole length, normal ventral epithelium on its ventral surface, which faces the dorsal surface of the host. Similarly in the case of Figure 66, a graft in reversed dorsoventral orientation, the graft outgrowth possesses normal dorsal epithelium on its lower surface throughout its length although it arises from the ventral surface of the host. The outgrowths induced from the host body are covered with the epithelium of the surface from which they arise.

Some seventy grafts of postpharyngeal pieces into the pharyngeal region were made with normal orientation. In cases of complete union the graft gave rise to more or less dorsal elevation and migrated posteriorly, while new tissue and a new pharynx developed anterior to it in the region where it was implanted. Figure 68 shows a case of this sort, the dorsal elevation being shown as bent over to one side and the area of new tissue indicated by shading. This direction of migration and the position of the new pharynx in relation to the graft are exactly the opposite of those observed in the grafts of prepharyngeal pieces into the pharyngeal region (see p. 38).

In seventeen cases grafts from the middle postpharyngeal region into the pharyngeal region with normal anteroposterior and reversed dorsoventral orientation united with the host body and developed



as shown in Figures 69 and 70. As the figures indicate, the grafts developed an elongated growth on the dorsal surface of the host and migrated from the pharyngeal region, where they were implanted, almost to the posterior end of the host body. The growth represents a small planarian body, ventral surface uppermost, and attached by part of its dorsal surface to the dorsal surface of the host. In a few cases a normal head was present (Fig. 69); a few others possessed more or less inhibited heads; but the majority were headless (Fig. 70).



FIGS. 68-70.—Homoplastic grafts of triangular pieces from postpharyngeal into pharyngeal region. *Planaria dorotocephala*.

Fig. 68, union complete. Graft elevation has migrated posteriorly and original region of implantation is filled in with new tissue (indicated by shading) and has developed a new pharynx.

Figs. 69 and 70, normal anteroposterior, reversed dorsoventral orientation. Grafts have migrated posteriorly and have developed into small planarian bodies. Fig. 69, with normal head; Fig. 70, headless. The original region of implantation and the path of migration are filled in with new tissue (indicated by shading) in which a new pharynx has developed in each case.

#### DISCUSSION

*Determination of reorganization in the host body by the ganglionic grafts.* The most important result of the experiments thus far is the demonstration of the ability of the ganglionic graft to induce more or less extensive reorganization in the host body. Size of the

graft, degree of union with the host, and apparently also the physiological condition of the graft in relation to that of the host are factors concerned in determining whether or not the graft induces reorganization. The smaller the graft, the more frequently it is resorbed without inducing reorganization. Also, when some part of the graft fails to unite with the host tissue, its own dorsal and ventral epithelium unite with each other, and the head which develops possesses both dorsal and ventral epithelium and is more frequently normal than the head which develops when union is complete. When the epithelia of the graft unite completely with those of the host, the head which develops is not normal, being without cephalic lobes, usually monophthalmic, and covered with the epithelium characteristic of that surface of the body from which it develops. Even such heads, however, induce more or less reorganization in the host body; but this inducing action is less rapid and often less extensive than that of a normal head. It appears probable that such differences in the reorganizing ability of the graft head are due to differences in its physiological condition.

The heteroplastic transplantations between *Planaria dorotocephala* and *P. maculata* show that the action of the ganglionic graft in inducing reorganization is not species-specific. Ganglionic grafts from each of the two species induce reorganization in the other species, although the data indicate at present that the ganglionic graft from *P. dorotocephala* is somewhat more effective in *P. maculata* than vice versa. It is difficult, however, to obtain really demonstrative data concerning this point because of the differences between the two species. *Planaria dorotocephala* usually becomes larger than *P. maculata* and has a larger head. If we use animals of the same size as donor and host, the individuals of *P. dorotocephala* are probably physiologically younger than those of *P. maculata*; and this difference may play a part in determining the efficiency of the graft. If, on the other hand, animals of different size are used, the grafts from the two species are either of different size or do not represent corresponding body regions. If the *P. dorotocephala* graft is actually more effective in *P. maculata* than vice versa, it is not clear whether the difference is due to differences in the grafts or in the reactivity of the host tissues of the graft.

The reorganization induced in the host body by the graft head appears in two different forms. That part of the prepharyngeal region which develops in relation to the graft head develops as an outgrowth from the host body; while in cases in which a pharynx and postpharyngeal region is reorganized by the graft, they develop in the host body without outgrowth (Figs. 24, 26-29, 34-37, 39, 40). In no case observed has the postcephalic outgrowth represented more than the prepharyngeal region, and it usually does not represent the whole prepharyngeal region. At any given level the maximum outgrowth is never longer than that portion of the host body anterior to the level of implantation, and it may be shorter according to the degree of development of the graft head.

The induced postcephalic outgrowth is not normal in its structural characteristics even when the head is normal. It is usually more or less cylindrical in transverse section and is covered with the epithelium characteristic of that surface of the host body from which it arises. In many cases it contains an elongated, more or less tubular invagination from the opposite body surface, and this invagination is lined with the epithelium characteristic of that surface. In the case of heteroplastic grafts the epithelia of the induced postcephalic outgrowth are those of the host, not the donor species. The question may perhaps be raised whether this induced outgrowth really represents a postcephalic region. As regards this question, perhaps the most conclusive evidence that this outgrowth is physiologically a postcephalic region is that even when it is tubular in form reorganization of the host body with development of pharyngeal and postpharyngeal regions may be induced through it. Apparently the induced outgrowth is a more or less radially symmetrical postcephalic region, its radial symmetry resulting from the fact that it develops from either the dorsal or the ventral surface of the host body. Evidently the dorsoventrality of the normal graft head does not induce transformation of dorsal into ventral or ventral into dorsal epithelium in the host. Moreover, in many cases, the graft head itself is essentially radially symmetrical. Certainly in such cases no factor is present which could determine dorsoventrality in the induced outgrowth.

When a ganglionic graft is implanted into the prepharyngeal re-

gion of the host, the induced postcephalic outgrowth never includes pharyngeal or postpharyngeal regions, and apparently represents at most only that region of the body corresponding to the region of the host body anterior to the level of implantation. When reorganization of the host by the graft has taken place to this level, it evidently does not continue further because the more posterior levels of the body are already represented in the host; and since, if the effect of the graft extends to these regions, it could determine only the organs that are already present, the graft does not determine reorganization in them. When ganglionic grafts are implanted in the postpharyngeal region, the situation is very different, as will appear.

With the ganglionic grafts in the prepharyngeal region, the visible reorganization induced by the graft does not extend in the host body beyond the base of the postcephalic outgrowth; but when such grafts are implanted in the pharyngeal or postpharyngeal region, more or less reorganization may occur in the host posterior to, and often in the case of postpharyngeal grafts both posterior and anterior, to the postcephalic outgrowth. This reorganization consists in the development of a new pharynx and a corresponding reorganization of the gut. When it takes place anterior to the graft level, it involves complete reversal of polarity in the part of the host body concerned; while still farther anterior, the original polarity may still persist. In such cases three polar axes are present in the host body: in the more anterior region a part of the original axis; then a new polarity reversed in direction which is determined by the graft; and posterior to the graft level a polarity which coincides in direction with the original but is nevertheless a new polarity determined by the graft, since the development of a new pharynx and extensive reorganization are involved. In Figures 26-29 and 34-37, for example, and in other cases not figured, these three polarities exist. In some cases when the anterior end of the host is removed, the polarity is completely reversed at levels anterior to the graft, and head formation is inhibited at the original anterior end or it may be transformed into a posterior end (Figs. 27, 28, 35).

The fact is to be emphasized that neither the postcephalic outgrowth nor the reorganization of pharyngeal and postpharyngeal region in the host body represent a regeneration in any strict sense.



The development of the postcephalic outgrowth is much slower than reorganization, and no "new" or embryonic tissue is visible in it. Histological study of its development is not yet complete. Still less is the reorganization of pharyngeal and postpharyngeal regions a regeneration. It takes place very slowly without essential change of form of the body, though it undoubtedly involves cell division and growth in the development of the new pharynx and the reorganization of the gut. It is a familiar fact that in the reconstitution of postpharyngeal pieces the development of the new pharynx and postpharyngeal region represents the same sort of reorganization that is induced by the ganglionic graft. In both cases a head region is brought into or near to the postpharyngeal region and induces its transformation. That the factors involved in such reorganization must differ very considerably from those concerned in the regeneration of new tissue from a cut surface seems evident.

The results obtained with these ganglionic grafts, both homoplastic and heteroplastic, demonstrate very clearly the physiological dominance of the ganglionic region in development. Evidently the ganglionic region is the primary factor in determining and localizing the various postcephalic parts. It is even able to determine and localize such parts in a direction opposed to a polarity already existing. In short, it is an "organizer" in the sense in which Spemann and his co-workers have used the word.

Moreover, the ganglionic graft is not only an organizer, but it may prevent the development of a head at an anterior cut surface of the host body a considerable distance anterior to the level of implantation. This inhibition of the host head is probably simply one aspect of the organizing effect of the graft, that is, it inhibits or prevents head formation because it determines conditions in the parts concerned which favor or determine development of other parts than a head. In some cases this effect is merely sufficient to inhibit head formation so that a teratophthalmic, a teratomorphic, an anophthalmic, or even no head at all develops instead of a normal head. The ganglionic grafts show all degrees of this effect from mere partial inhibition of head development to complete transformation of an anterior into a posterior end (Figs. 27, 28, 35, 36).

When the ganglionic graft is implanted at or near the level of the

postpharyngeal region at which fission usually occurs, fission at that level is prevented in all cases observed, and the region of fission is reorganized by the graft (Figs. 27, 28). In some cases in which the graft was implanted posterior to the level at which fission usually occurs, fission at the usual level took place soon after implantation, but the graft head prevented the development of a head at the anterior end of the fission piece and functioned as the head of the piece.

In many cases of ganglionic grafts in the postpharyngeal region it was found that the effect of the graft head on a cut surface of the host body anterior to its level developed only very gradually. Often a normal head developed after the first removal of the anterior end of the host, a somewhat inhibited head after the second removal, and complete prevention of head development after the third removal. In some cases the effect develops more rapidly, in others less rapidly, in still others it remains slight or is apparently absent and there is no reversal of polarity. Such differences are apparently correlated to some extent with differences in degree of development of the graft head. In general, the more nearly normal the graft head, the greater its effect in preventing head formation at more anterior levels of the host body and in reversing polarity. The gradual development of this dominance and determining action of the graft head suggests that it may be associated with a gradual reorganization of the nervous system progressing from the graft head to a greater or less distance from the host body.

The question may be raised as to the factors concerned in determining that the induced prepharyngeal region develops as an outgrowth from the host body while the induced pharyngeal and postpharyngeal regions develop through reorganization within the host body, that is, without outgrowth. A complete answer to this question cannot be given, but attention may be called to certain points. First, the development of the induced postcephalic outgrowth occurs more rapidly than the reorganization in the postpharyngeal region. Apparently the ganglionic graft induces more or less outgrowth before the reorganization of more posterior levels has time to occur.

Second, the figures show that the length of this outgrowth is variable, particularly in postpharyngeal implantation, even when the level of implantation is approximately the same; and also, that the

scale of organization of the new axis or axes differs widely in different cases. The induced pharynx or pharynges may arise at a considerable distance from the base of the postcephalic outgrowth or almost at its base. Apparently a relation exists between the effect of the graft in inducing outgrowth from the host body and in inducing reorganization in the host body posterior or anterior to the outgrowth. In other words, the postcephalic outgrowth may represent physiologically a larger fraction of the new polar axis in some cases than in others, and the reorganization in the host body posterior or anterior to the level of implantation apparently represents the levels of the new axis which are not represented in the postcephalic outgrowth.

Third, the rapidity with which the postcephalic outgrowth develops and the scale of organization in the new axis are probably determined by the degree to which the graft head influences the host, and they in turn determine how much of the new axis is represented by the outgrowth.

Fourth, the dominance of the graft head in postpharyngeal implantation does not necessarily extend to the posterior end of the host body. Most of the ganglionic grafts in the postpharyngeal region were implanted at or near the level at which fission would normally occur. In such cases the graft always prevents the occurrence of fission. In the normal individual the anterior end of the second zooid is only a short distance posterior to the mouth, and the same is probably true in individuals like Figures 27, 28, 35, 36, and 37. Thus far no attempt has been made to determine whether the posterior end of the host body is to some extent physiologically isolated from the dominance of the graft head. The reorganization does not afford any evidence on this point, since this region remains a postpharyngeal region even after the induced reorganization; and physiological isolation cannot be expected to alter its structure since the structure of the posterior zooid region is not appreciably altered in the normal individual.

Thus far no case of fission in a transformed anterior cut end of the host body after removal of more anterior portions (Figs. 27, 28, and 35) has been observed; and such cases are not to be expected, for, if the dominance of the graft head is sufficient to prevent formation of

a head and to transform the anterior end into a posterior end, it is evident that the degree of physiological isolation in such a region cannot be sufficient to permit fission unless considerable increase in length or a decrease in dominance occurs.

In short, the results of ganglionic grafts in the postpharyngeal region indicate that the graft head determines a new polar organization which is represented in part by the postcephalic outgrowth, in part by reorganization in the host body; that the new axis thus determined may differ greatly in length, that is, in scale of organization in different cases; and that the portions of the axis represented respectively by the postcephalic outgrowth and the reorganization in the host body also differ in different cases with the degree of dominance of the graft head over the body of the host.

*The grafts of postcephalic regions.*—The data presented concerning the grafts of postcephalic regions serve chiefly to indicate something of the variety of results attained with such grafts. The figures show that under certain conditions such grafts may determine a very considerable dorsal or ventral elevation or outgrowth even when union is complete. Very few heteroplastic grafts of postcephalic regions have been made as yet, and it is impossible in most cases of homoplastic grafts to determine how much of such outgrowths develops from the graft itself and how much is induced from the host body. In the case of grafts of the pharyngeal region into prepharyngeal levels (Figs. 52 and 53), the position of the mouth suggests that the posterior side of the outgrowth has developed from the host body; but in other cases there is no landmark.

Unquestionably these elevations or outgrowths represent more or less reorganization, which may involve to a greater or less extent regions of the host body adjoining the graft; but what the elevation or outgrowth represents physiologically and what conditions determine its development the data at hand do not show. It must be left for future investigation to determine whether these grafts of postcephalic regions are able, in certain cases, to determine some degree of definite reorganization in the host body beyond that associated with the union of the graft and host tissues.

When union is incomplete, the postcephalic graft may develop a head and a postcephalic outgrowth or a posterior end. Undoubtedly



the heads in such cases possess the same ability to reorganize the host body as do the heads arising from ganglionic grafts; but in these cases the first effect of the head is on the graft itself, and this may be induced by the head to develop into a postcephalic outgrowth. Such reorganization is similar to that which occurs in the reconstitution of an isolated piece. Unfortunately, no case of heads developing from postcephalic grafts in consequence of incomplete union have been observed in postpharyngeal implantation. Consequently, it is not known whether such heads will determine reorganization and reversal of polarity in the host body as do the heads which develop from ganglionic grafts. There is, however, every reason to believe that they will have the same effect.

The migrations of the postcephalic grafts present an interesting problem. In most cases the postcephalic graft implanted into a different body level with normal orientation appears to migrate toward the level from which it was taken, and new tissue develops in the region of implantation. Orientation, however, is a factor in determining the direction of migration. Grafts of the pharyngeal region implanted into the same region in reversed anteroposterior and normal dorsoventral orientation migrate in the posterior direction (Figs. 57-59) instead of remaining in the pharyngeal region, and new tissue and a new pharynx develop in the pharyngeal region of the host. Apparently the graft is not simply forced out of the position of implantation by the development there of new tissue, but is itself a factor in the migration. Further study of these migrations is planned in the hope of throwing some light on the factors concerned.

*The polarity and dorsoventrality of the graft.* Apparently the dorsoventrality of the graft persists in all cases in which it is not resorbed, and in many cases it is evident that the polarity also persists. But in those cases among the ganglionic grafts in which the head region is a rounded, bluntly pointed structure with a single eye, it is impossible to determine whether the original polarity of the graft persists or not. In cases of postcephalic grafts in reversed anteroposterior and normal dorsoventral orientation it is often possible to determine by later operation whether or not the original polarity persists. Such operations show that in certain cases the original polarity of the graft is obliterated and a new polarity is determined,

but these cases are not described in the present paper. In post cephalic grafts in reversed anteroposterior and reversed dorsoventral orientation the original polarity apparently always persists. Evidently the orientation and degree of union of the postcephalic graft in relation to the host are factors in determining whether or not the original polarity of the graft persists.

*The invagination.*—In the ganglionic grafts an invagination from the side of the body opposite the outgrowth is of frequent occurrence, as has been shown above. This invagination may develop from either the dorsal or ventral surface and ranges from a mere depression to a more or less tubular invagination, sometimes extending the whole length of the induced postcephalic outgrowth. In grafts of pieces from postcephalic regions it is also of frequent occurrence, and shows the same range of form; but in certain cases does not persist indefinitely.

This invagination presents another interesting problem. Its development appears to be correlated with the more or less radial character of the outgrowth. The graft determines a localized region of growth in a direction more or less at right angles to the longitudinal body axis. This growth involves not merely the dorsal and ventral surface but the whole thickness of the body, and occurs in all radii in the mediolateral plane of the body in the region where it is localized. The consequence of these conditions is that the outgrowth is more or less cylindrical or conical in form but possesses a dorsoventral differentiation along the radii of its transversed section. Its dorsal surface may be external, its ventral, internal; or vice versa. It appears that such a pattern results simply from the localization of a region of growth involving more or less the whole thickness of the body and at right angles to the polar axis and the mediolateral plane. The outgrowth is more frequently dorsal than ventral; consequently the invagination is more frequently ventral than dorsal. This probably results from the fact that the ventral surface is in contact with the substratum which offers some resistance to the outgrowth.

*The controls.*—The hosts in which the grafts did not "take" have been used as controls. In most of these, the opening made by the removal of a piece for the insertion of the graft contracts, new tissue develops in it, and the region finally becomes indistinguishable from

adjoining regions. When the piece removed represents the pharyngeal region, a new pharynx develops. When the piece removed is almost the whole width of the body, separation of the parts anterior and posterior to the level of operation often occurs and the parts undergo reconstitution in the usual way. Occasionally the opening left by the removal of the piece does not entirely close, and a head develops in it from the cut surface which faces in the anterior direction.

*Transplantation and reconstitution.*—In conclusion it may be pointed out that there are certain resemblances between transplantation and the reconstitution of isolated pieces. This is particularly the case with regard to the ganglionic grafts as compared with the regeneration of a head on an isolated piece and its reorganizing effect on levels of the piece posterior to it. Child (1929*b*, pp. 38 and 39 and references there cited) has shown that an isolated piece which remains headless never gives rise to any part anterior to the level of the body from which it was taken, but that, if even a rudimentary head develops, reorganization of the more anterior parts of the piece into those levels of the body which originally lay between the level of the piece and the head takes place. Even in the absence of a head, however, the piece is able to develop all parts representing levels posterior to its level in the original body. This fact indicates that physiological dominance in the reconstitution of *Planaria* acts chiefly in the direction from anterior to posterior. Child has also shown that the scale of organization of the body regions determined by the regenerating head may vary greatly with the degree of development of the head (Child, 1929*b*, pp. 38 and 39 and citations). Evidently the regenerating head is an "organizer" as well as the grafted head or ganglionic region. The chief difference between the results obtained with the ganglionic grafts and the results in reconstitution is that, in the case of the graft, the new head may develop either on the dorsal or the ventral surface of the host and be entirely covered with dorsal or ventral epithelium. Even in such cases it is able to bring about reorganization in the body of the host. In such cases, however, the postcephalic outgrowth may also be completely covered externally with dorsal or ventral epithelium and may contain a tabular invagination lined with the epithelium of the opposite

surface. But even these outgrowths apparently function as postcephalic regions, since further reorganization of more posterior regions in the host body may take place through them. In short, when a head develops at the anterior end of an isolated piece, the effect, as regards reorganization in regions posterior to the regenerating head, is very similar to the effect of a head or ganglionic region grafted at the same body level.

In the case of grafts of postcephalic regions the resemblance to the reconstitution of isolated pieces is not as great. When complete union between graft and host occurs, the graft may or may not give rise to an outgrowth—size of graft, level of body from which it is taken, and level of implantation being factors in determining the result. In other words, these factors determine whether or not the graft is able to grow at the expense of the host and perhaps to bring about some degree of reorganization. Such a graft, however, does not develop a head; and even if it does determine some degree of reorganization, it is much less effective than the ganglionic graft. If, however, the postcephalic graft does not unite completely with the host and develops a head, this head apparently possesses the same ability to reorganize the body of the host as does the head which develops from the ganglionic graft.

In general, the results of the experiments on transplantation agree with the data on reconstitution in showing that the head region is the chief or primary region of physiological dominance in the body.

#### SUMMARY

1. Grafts of pieces from the ganglionic region of *Planaria dorotocephala* or *P. maculata* implanted in prepharyngeal levels of the host body, if above a certain size, may give rise to heads and determine the development from the host body of a postcephalic outgrowth.

2. Ganglionic grafts implanted into postpharyngeal levels of the hosts not only develop heads, and may determine postcephalic outgrowths from the host body, but also determine a further reorganization in the host body with the development of a pharynx and postpharyngeal region.

3. The reorganizing influence of the graft head may extend in the host body not only posterior but also anterior to the level of the post-



cephalic outgrowth; that is, it may determine two polarities in opposite direction in the host body, one of which represents a complete reversal of the original polarity.

4. The head region which develops from the ganglionic graft is an "organizer" or a "reorganizer" - in other words, a dominant region which initiates and determines the development of postcephalic regions.

5. The scale of organization (that is, the length of the new axis or axes determined by the graft head) varies in different cases.

6. The reorganizing influence of the graft head is not species-specific. Ganglionic grafts from *P. dorotocephala* induce reorganization in *P. maculata*, and vice versa.

7. The head which develops from the ganglionic graft may be normal in structure when union between graft and host is incomplete and dorsal and ventral epithelium of the graft unite with each other. When union is complete, the graft head is a more or less conical or rounded structure, often with a single eye and without cephalic lobes, and is completely covered either with dorsal or ventral epithelium according to the surface on which it develops. Even such heads, however, are able to induce some degree of reorganization in the host.

8. The postcephalic outgrowth induced by the graft head is not a normal postcephalic region. It is more or less cylindrical and is covered either with dorsal or ventral epithelium, according as it develops from the dorsal or ventral surface of the host; and frequently, also, an invagination from the opposite surface of the host body extends a greater or less distance into the outgrowth. This invagination is lined with epithelium characteristic of the surface from which it arises. Consequently the postcephalic outgrowth may be tubular, and possesses dorsal epithelium on its outer and ventral epithelium on its inner surface, or vice versa.

9. The fact that the reorganization of other parts of the host body into pharyngeal and postpharyngeal regions, and even reversal of polarity in the host body, is determined by the graft head through the postcephalic outgrowth indicates that this outgrowth represents physiologically the more anterior postcephalic portion of a polar axis.

10. Various results obtained with grafts of pieces from prepharyngeal and pharyngeal regions are described. When union is complete, such grafts may give rise to headless outgrowths with invagination from the opposite body surface. In cases of incomplete union, reconstitution of a head and reorganization of the graft may occur.

11. In certain cases, the postcephalic grafts migrate from the region of implantation in the host body, and new tissue develops in the region of implantation. With grafts from a given body level implanted in a given level of the host with a given orientation, the direction of migration is apparently always the same. Region of origin and of implantation and orientation of the graft with respect to the host are all factors in determining the direction of migration.

12. In general, when not resorbed, the grafted pieces retain their original dorsoventrality and frequently their original polarity. But in many cases it is impossible to determine whether or not the original polarity persists, and in certain cases in postcephalic grafts it is obliterated and a new polarity determined.

13. The invagination from the opposite side of the body into the outgrowth apparently results from the fact that the graft becomes or induces a localized region of growth in a direction more or less at right angles to the polar axis and the mediolateral plane of the host body and involving the whole thickness of the body. The consequence of such localized growth is the development of an outgrowth from either the dorsal or the ventral surface and a corresponding invagination from the opposite surface.

14. The hosts in which the grafts did not "take" have been used as controls. In most of these the opening made by the removal of a piece for the insertion of the graft contracts; new tissue develops in it; and the region finally becomes indistinguishable from adjoining region. If it is in the pharyngeal region, a new pharynx develops. When the piece removed is almost the whole width of the body, separation of the parts anterior and posterior to the level of operation often occurs and the parts undergo reconstitution in the usual way. Occasionally the opening left by the removal of the piece does not entirely close, and a head develops in it from the cut surface which faces in the anterior direction.

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